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The *Neoperla* of Sumatra and Java (Indonesia)

(Plecoptera: Perlidae)

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Abstract

Sumatra and Java are inhabited by a distinct fauna of shared or closely related species of *Neoperla* belonging to several phyletic lines. Of the 19 named species, 16 occur on Sumatra, 9 on Java. The fauna appears to be of mainland origin with probable relatives in South India. Limited recent faunal exchange is indicated by presence of three of the species on the Malayan Peninsula. The most expansive species, *N. fallax*, extends to North Thailand. In the east, several species reach Bali or even Lombok. A number of literature records of Sumatran or Javan *Neoperla* from other parts of Asia were based on misidentified specimens.

Known stonefly habitats in Sumatra and Java are on or along the volcanic mountain belt surrounding the Sunda Plate in the west. No Plecoptera have so far been recorded from the Sunda Plate lowland portions of Sumatra. This probably explains the lack of close faunal relations with Borneo and the Philippines which are part of the Sunda Plate properly speaking.

Incomplete knowledge, especially of Asian species, presently precludes subdivisions of the very large genus *Neoperla* into formally named subgenera. A general division of *Neoperla* species into the *clymene*-group (North America, Asia, Africa) and the *montivaga*-group (Asia) is proposed. These two major groups and several of their subgroups are defined. The position of *N. tenuispina* in genus *Neoperla* remains uncertain.

Based on study of types of all previously named taxa (several lectotypes designated) the following species are recognized, described, illustrated and identified in keys (adults only): *N. aeripennis* (ENDERLEIN) (= *Ochthopetina violaris* ENDERLEIN, new synonymy); *N. caligata* (BURMEISTER) (neotype designated); *N. sumatrana* (ENDERLEIN) (= *N. enderleini* ILLIES, not *N. sumatrana* Klapálek); *N. propinqua* spec. nov.; *N. aliqua* ZWICK; *N. rigidipenis* spec. nov.; *N. primitiva* GEIJSKES (with *N. p. primitiva* GEIJSKES, *N. p. inutilis* ZWICK, stat. nov. (= *N. sumatrana* Klapálek, not ENDERLEIN), *N. p. separanda* ssp. nov.); *N. jacobsoni* Klapálek; *N. vesperi* spec. nov.; *N. distincta* spec. nov.; *N. luteola* (BURMEISTER); *N. simplicior* NAVÁS; *N. fallax* Klapálek; *N. lieftincki* spec. nov.; *N. affinis* spec. nov.; *N. pilosella* Klapálek (= *N. rubens* Klapálek, new synonymy; = *N. mitis* Klapálek, new synonymy); *N. stueberae* spec. nov.; *N. illiesi* spec. nov.; *N. tenuispina* Klapálek. Unassociated females of 4 species are given provisional letter designations.

N. laminulata (ENDERLEIN) is a doubtful name, the type cannot be identified to species. *N. dolichocephala* Klapálek is a Malayan species, records from the islands are not confirmed. Species from Sumatra and Java formerly included in *Neoperla* but presently assigned to different genera are: *minutissima* ENDERLEIN and *flaveola* Klapálek, both *Phanoperla*; *modiglianina* NAVÁS, *Etrocorema*; *reducta* GEIJSKES, *Chinoperla*.

In recent years, studies of inner penis armature, vaginal sclerites, and egg chorion have revealed that characters previously used to distinguish species of *Neoperla* (e. g., colouration, wing venation, ocellar indices, even external genitalia) are usually too variable or too uniform to permit identifications. Most of the many species named in the past are inadequately known and cannot be recognized from existing descriptions. Recent studies indicate that contrary to what had been expected (ILLIES 1966) many more species actually exist than have been named so far. Before material can be identified at least species previously named from the same geographical area have to be redescribed from types. In the

past, the two sexes of a single species have sometimes inadvertently been given different names. To recognize this, much material is usually needed because in most cases conspecificity of sexes can be inferred only from circumstantial evidence. In order not to increase existing problems I have adopted the policy not to name species known in the female sex only, even though most females with eggs can be identified as reliably as can be males.

The insular faunas of Sumatra and Java are sufficiently distinct to merit separate treatment. Study of many *Neoperla* from the Oriental region has shown me that the two islands share a number of similar or closely related species. Faunal connections with the neighbouring Malay Peninsula and Borneo are minimal or non-existent in *Neoperla*, compare below. A fairly rich material of *Neoperla* from Sumatra and Java has been available. Types of all Neoperlini named from these islands have either been redescribed in recent years (ZWICK 1973, 1982a, b) or have been examined now. It is therefore possible to present a reasonably complete synopsis. Still, some species are insufficiently known and remain unnamed, better material of several others that have been named would be desirable. There appears to be no point to wait for these better collections to be made. Habitat destruction is said to progress rapidly also in this part of the world and its fauna should become known while it still exists.

The *Neoperla* of Sumatra and Java are not of a single ancestral stock but belong to several phyletic lines that must have immigrated independently from the Asian mainland. In view of our scanty knowledge of mainland *Neoperla* it is difficult to name the closest relatives and probable areas of origin for the insular fauna. The group of *N. luteola* as well as *N. illiesi* appear to have relatives in south India. Limited faunal exchange has occurred across the Strait of Malacca. *N. distincta* is widespread on the mainland and appears to have reached the north of Sumatra from there. *N. fallax* has all its relatives on the islands and probably spread in the other direction. *N. spec. J* which occurs in Sumatra and Malacca is insufficiently known. The fauna of Sumatra, which is closer to the mainland, appears to be more diverse than that of Java. In the east, *N. luteola* occurs on Bali, *N. primitiva* extends to Lombok and *N. fallax* may also be present there.

In *Neoperla*, there appear to be no faunal connections between Sumatra and Java on the one hand and Borneo on the other. There are neither shared nor very closely related species. This situation is remarkably different for the one reported for fishes (DE LATTIN 1965) which are largely the same in south Sumatra and west Borneo. Rivers in these areas have once formed a single drainage system. Its drowned valleys on presently submerged parts of the Sunda Plate can still be detected (TIETZE 1968–72). While distribution of fishes clearly depends on drainage systems spread of the rheophilous and predominantly montane stoneflies occurs in their aerial adult stage. They disperse from one headwater stream to the next in mountain areas, regardless of drainage systems. In fact, most stonefly localities known in Sumatra and Java are on or along the volcanic inner arch of mountains surrounding the Sunda Plate. Sumatra and Java have largely been formed by this mountain system which has its highest peaks there. It extends further east through the Smaller Sunda Islands but has no connection to Borneo. The Neoperlini of Borneo seem to have close affinities with those of the Philippines, which like Borneo are part of the Sunda Plate properly speaking.

Technical notes

Study of the penis is necessary and eversion of its retracted inner sac is desirable for identification of males. Pinned specimens are relaxed in a moist chamber for about 1 hr. The abdominal tip is then cut off. It is briefly dipped into alcohol to facilitate wetting with approx. 10% KOH to which it is transferred for 45–60 mins. Then the penis is removed. When surrounding membranes have been detached the penis is held at its base with fine forceps and wiped from base to tip with a bent needle tip. Release forceps occasionally to permit entry of fluid into base of penis. The half macerated gelatinous muscles inside the penis are thus used to expel and expand the inner sac within a few seconds. The penis is afterwards returned to KOH and left with the abdomen until completely cleared. The cold maceration recommended here gives better results than my former technique (ZWICK 1982a).

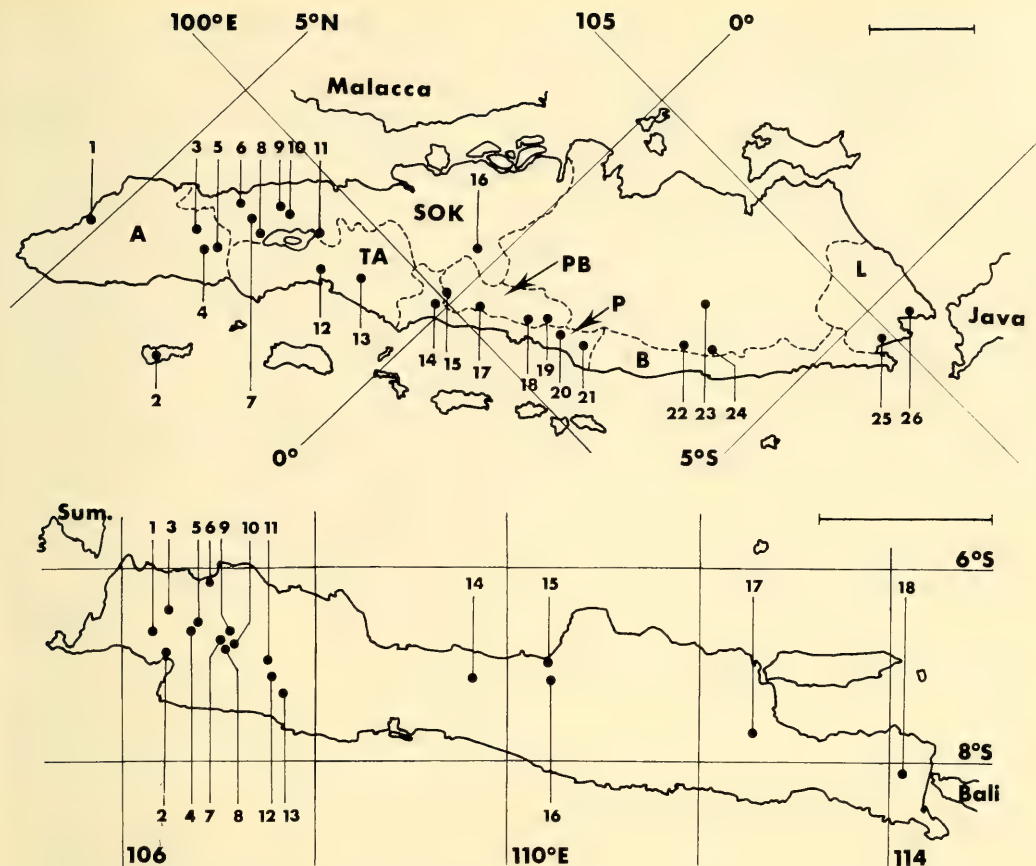


Fig. 1: Approximate location of several collecting sites and points of reference on Sumatra (top) and Java (bottom), note that scale length is 200 km for both maps.

Sumatra: the location of a few collecting sites is not known, but their approximate position can be inferred from lable references to colonial regions and colonial administrative units; the boundaries and designations of some of these are therefore indicated: A- Atjeh (= Aceh); B- Benkulu; L- Lampungs (= Lampung); P- Padang Lowland; PB- Padang Highlands (Padangse Bovenland); SOK- Sumatra's Oostkust (= Sumatra S.O.K.); TA- Tapanuli; Sumatra's Westkust (= Sumatra S.W.K.) is composed of P + PB + TA.

Sumatra:

- | | |
|--|---|
| 1 – Bireuen (5.12 N/96.42 E) | 10 – Pematangsiantar (2.58 N/99.03 E) |
| 2 – Island Simalur | 11 – Balige (= Balighe of MODIGLIANI) (2.20 N/99.04 E) and Forest of Si Rambé |
| 3 – Mt. Bandahara (3.45 N/97.47 E) | 12 – Pangherang Pisang (between Sibolga and Tarutung) |
| 4 – Kutatjane (3.31 N/97.47 E) | 13 – Padangsidempuan (1.23 N/99.16 E) |
| 5 – Balelutu (3.43 N/97.38 E) Alas Valley | 14 – G. Teleman (= G. Talakmau = G. Ophir) |
| 6 – Serdang District | 15 – Lubuksikaping (= Loeboek Sikaping) (0.08 N/100.10 E) |
| 7 – Sibolangit (3.19 N/98.55 E) | 16 – Bangkinang (0.21 N/101.02 E) |
| 8 – Mt. Singgalang (= Dolok Singgalang, 2.57 N/98.37 E) | 17 – Fort de Kock (Bukittinggi) (0.19 S/100.22 E) |
| 9 – Deli (Dolok Merangir: 3.06 N/99.03 E); Soekaranda, type locality of several of ENDERLEIN's species, is also in Deli. | 18 – Alahanpandjang (1.05 S/100.47 E) |

- 19 – Balun, Muara Labu (= Muara Labuh)
- 20 – G. Kerintji, 3805 m (1.42 S/101.16 E); the Kerintji area is called 'Kurintji' (= Kur.) on labels of E. JACOBSON
- 21 – Muara Sako (= Muarasako, 2.07 S/101.13 E), 680 m
- 22 – Rimbo-Pendagang, Benkulen (= Rimbopen-dagang, 3.18 S/102.25 E)
- 23 – Muara Klingi (= Muaraklingi, 3.05 S/103.14 E) on the upper course of the Musi River
- 24 – Kepahiang (3.39 S/102.34 E)
- 25 – G. Tanggamus (5.25 S/104.42 E), Giesting (5.21 S/104.43 E)
- 26 – Pandjang and Wai Lima

Java:

- 1 – G. Limboeng (= G. Limbung, 6.34 S/106.27 E; another mountain by this name is at 7.30 S/107.47 E)
- 2 – Tjisolak (= Cisolak; 6.55 S/106.27 E); Palabuan Ratu (= Pelabuhan Ratu) is 12 km to the east
- 3 – Djasinga (= Jasinga; 6.29 S/106.28 E)
- 4 – G. Salak, 2211 m (6.42 S/106.44 E)
- 5 – Buitenzorg (= Bogor, ca. 250 m) (6.35 S/10.64 E)
- 6 – Batavia (= Djakarta; Jakarta)
- 7 – G. Pangrango (= Panggerango; 6.46 S/106.57 E), 3019 m
- 8 – G. Gede, 2958 m (6.47 S/106.58 E)
- 9 – Tjisarua (= Cisarua; 6.39 S/106.54 E), 900–1200 m
- 10 – Tjibodas (= Cibodas; 6.45 S/106.54 E), 14–1450 m
- 11 – Bandung (6.54 S/107.36 E)
- 12 – G. Malabar, 2342 m (7.08 S/107.34 E)
- 13 – G. Tjikorai (= Cikorai; 7.19 S/107.52 E)
- 14 – Dieng Mts. (7.15 S/109.55 E)
- 15 – Semarang (6.58 S/110.25 E)
- 16 – G. Ungaran (7.12 S/110.20 E)
- 17 – Ardjoeno (= Arguno; 7.45 S/112.34 E)
- 18 – Idjen-Plateau (= Jjen Pengunungan; 8.05 S/114.15 E)

Females are opened dorsally to remove eggs and inspect the vagina. The abdomen of relaxed dry specimens is cut off, and placed into 75% alcohol to remove eggs first. Unless really full of eggs abdomina have often to be soaked in water first, but then eggs tend to swell and burst. Afterwards the abdomen is cleared in KOH; this may sometimes also be necessary with specimens preserved in fluid.

Genitalia have been stored in glycerol in microvials or mounted in Euparal on transparent cellulose foil. As a rule, the genitalia preparations have been attached to the specimen pin. Sometimes, eggs have been mounted separately on glass slides. Figures in this paper are camera lucida drawings of specimens in glycerol (all male abdomina) or in permanent mounts.

The complete label information is contained in the lists of material below. Collector, housing institution of the collection (for abbreviations used, see 'Acknowledgements') and information on previous identifications are presented in parentheses. Oblique strokes separate texts on different labels of the same specimen. Notes on circumstances of collection and the like have been translated into English. Collecting dates have often been completed by adding the century and are presented in a uniform way: day, month (Roman numerals), year. Other additions (mainly area designations explained in fig. 1) appear in square brackets.

Most specimens have been collected between 1890 and 1935 while Sumatra and Java were part of a Dutch colony, the Netherlands' Indies. To facilitate orientation the more frequently listed localities and points of reference are shown on maps in fig. 1. The legend includes present Indonesian names, additional informations and comments. Accurate location of collecting sites is not known to me in all cases but approximate positions can be inferred by provinces and Dutch administrative areas mentioned on labels. The limits and names of some of these have therefore been included in the maps (after ANDREES: Allgemeiner Handatlas, 1899). There is some variation in spelling of names (in particular Dutch -oe = -u!), e. g.: G. = Goenoeng = Gunung, mountain; Gedeh = Gedé = Gedek = Gede, etc. Sometimes, it has also simply been difficult to decipher handwritten labels and a few of my interpretations differ from those of ULMER (1951). Descriptions and maps of some collecting sites are in THIENEMANN (1930) and especially RUTTNER (1930) and BYERS & CHAN (1978).

The distinctive characters of Neoperlini and their three presently recognized genera have been discussed recently (ZWICK 1982a). The only apomorphic character suggesting monophyly of genus *Neoperla* is the presence of a pair of strongly sclerotised raised knobs at the sides of the dorsally displaced basal penis opening. Extensions or other modifications on tergites 7 and 8 are probably also derived but too varied in structure (also not present in all species) to be useful for diagnostic purposes.

Neoperla species occur in North America, Asia, and the Afrotropical Region. In view of their vast number, subdivision of the genus or some arrangement of species into groups would be helpful and is attempted here. However, because specific characters of *Neoperla* have been recognized and described only recently, many species remain inadequately known and every grouping must therefore be somewhat preliminar. For this reason, no nomenclatorily valid subgeneric names are introduced, but some informal group designations are proposed instead.

Formal recognition of subgenera may later be desirable. Several names presently suppressed as synonyms of *Neoperla* will be available for this: *Ochthopetina* ENDERLEIN, 1909; *Javanita* Klapálek, 1909; *Tropidogynoplax* ENDERLEIN, 1910; *Formosita* Klapálek, 1914 (= *Formosina* Klapálek 1913, nec BECKER 1911); *Oodeia* Klapálek, 1921, *Neoperlops* BANKS, 1939, and *Simpliperla* WU, 1962. Unfortunately, these names are based on inadequately known type species, except *Ochthopetina* and *Javanita* the type species of which are members of the *aeripennis*-subgroup of the *clymene*-group, see below. *N. clymene* (NEWMANN, 1839) is the type species of *Neoperla* NEEDHAM, 1905 (by original designation).

Characters typical of the group to which a given species belongs are not repeated in the descriptions of individual species, unless they require some comment or specifications. Abbreviations used in descriptions are: HT-hemitergite(s) 10; S – sternite(s); T – tergite(s).

I. The *clymene*-group

Males in this group are distinguished by complete (though sometimes weak) sclerotisation of the tubular penis, except on an approximately circular ventrobasal area which remains soft. Basally from it, the sclerite is truncate and this transverse smooth edge can be used to recognize species with indistinct or reduced sclerotisation of the penis tube.

The eversible sac is only the armed basal section of a long cuticular lining extending from the tip of the everted penis through the penis and through its basal opening into the efferent ducts of the inner genitalia.

Females have a small and narrow vagina but the delicate transparent seminal receptacle is attached to a widened and often greatly prolonged stalk which is internally armed with basally directed spicules, at least in places.

Eggs are very variable in shape and structure and differ between subgroups.

Long tubular sclerotised penes and modified receptacular stalks are apomorphic and do not occur in other Neoperlini; they support the monophyly of this very large complex. Complete break-down into subgroups is not attempted, most species considered here can be assigned to one of the following two major subgroups.

I.1 The *aeripennis*-subgroup

Spinules on male T8 arranged in two separate bands, or in a single posteriorly forking band. Females with projecting subgenital plates. The widened armed part of the receptacular stalk is short and conical, comma shaped, its distal section is narrow and unmodified. Eggs are variously shaped, the chorion is reticulate or has patterns derived from reticulation, not striate.

This subgroup is endemic to the Oriental region; in addition to species described below it appears to include a few presently not well known ones from the south east Asian mainland. Females are easily recognized by their comma shaped receptacular stalks. Males of the more primitive species are quite similar to those in the following subgroup, except T8. The more derived members of the group have soft annulate penes which are often angularly bent and then rest on their side. There is a pronounced tendency for modified hemitergites 10 and/or sternites 9.

Some species are amazingly variable, identifications of males are sometimes difficult; females without eggs cannot be identified to species. When more material and definitely associated females will be available (presently, all associations tentative, except *P. aeripennis*), the status of some taxa may have to be re-evaluated.

I.1.1 *Neoperla aeripennis* (ENDERLEIN) (Figs. 2a-e)

1909 *Ochthopetina aeripennis* ENDERLEIN, Stett. ent. Ztg. 70: 325, fig. 13.

1909 *Ochthopetina violaris* ENDERLEIN, Stett. ent. Ztg. 70: 325, fig. 14. – New synonymy.

1973 *O. aeripennis*, *O. violaris* – ZWICK, Annls. Zool. Warszawa, 30: 496, figs. 55–57 (lectotypes designated).

Material examined: Java: 1 ♀, Java, paralectotype of *O. violaris* (MCZ); 2 ♀♀, Salak, 800 m, VII. 1920 (D. v. L.; ML); 1 ♂, Panggerango, Tjisaroea, 11. XI. 1931; 1 ♂, 1 ♀, in copula, Gedeh, Tjibodas, Tjiwalen, 1400 m, 29. VI. 1933; 1 ♂, Priangan, G. Limboeng, 1000 m, 10. VII. 1934 (all LIEFTINCK; ML); 1 ♂, 1 ♀, Tjibodas, 1400 m, VIII. 1921; 1 ♂, same locality, 22. V. 1935 (v. D. VECHT; all ML). 1 ♀, Java; 1 ♀, Java occid./FRÜHSTORFER/Greifswald; 1 ♂, Gedeh, Dr. O. STAUDINGER V[edit] (all NMP, labelled “*fusca* KLAPÁLEK”). Sumatra: 1 ♂, Pangherang-Pisang, X. 1890–I. 1891 (MODIGLIANI; MCG).

Wings of ♂♂ 13.5–15.0 mm, of ♀♀ 14.5–23.0 mm long. Rs with 2 or 3 main branches, the anterior one or two distally forked. Ocelli small to very small, 2–4 diameters apart. Upper side dark brown with more or less distinct blue sheen. Lower face of head, thorax and bases of femora (extension variable) yellow. The darkest part is the area between the ocelli; tentorial calluses, antennal sclerites and lateral portions of the M-line may be yellowish.

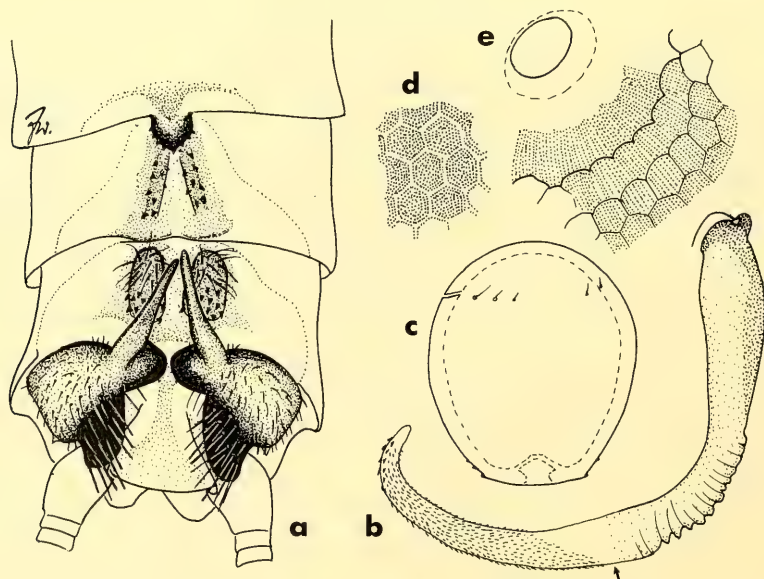


Fig. 2: *Neoperla aeripennis* (ENDERLEIN): ♂ abdominal tip (a), everted penis; arrow marks level to which the inner sac can be retracted; egg (c), with details of chorion sculpture near greatest diameter of egg (d) and on anchor pole, oblique side view (e).

♂: Sternites simple, S9 broadly truncate. Process of T7 small, pentagonal, strongly sclerotised, spinuliferous along edges and below. Spinules on central sclerite of T8 on two diverging ribs running parallel to edge of sclerite. T9 largely membranous, central sclerite large, with two strongly raised oval knobs each of which setose in front, spinuliferous behind. HT strongly sclerotised. Median lobe flat, very shining, no spinules at tip. Anterior process slender, straight, pointed. Each HT on its postero-median face with large horizontal extension, its outer face straight, inner side convex. Long erect brown setae on the base of this hard process extend across and beyond the bare tip. Cerci simple.

Penis tubular, sclerotisation reduced except dorsobasally, tube dorsodistally annulate, apex gently curved to ventral side. Inner sac about as long as the tube, densely covered with minute slender hooklets except at bare base. A few slightly larger hooks near tip apparent at magnification 50 ×.

♀: S8 with hardly projecting median sclerotised lappet several times wider than long but only about $\frac{1}{6}$ the segment's width. It is usually slightly bilobed, sometimes only two indistinct paramedian bumps appear on the distal edge of S8. Inner genitalia typical of the group, modified section of receptacular base very small, spicules in it few, appearing poorly sclerotised, difficult to see; compare figs. 55–57 of ZWICK (1973).

Egg: about 0.38 mm long, almost spherical, anchor pole a little narrowed, flattened. No collar; anchor (details unknown) inserts in a deep narrow central groove. At low magnifications chorion appears smooth, shining. In fact there are radial lines of very fine punctures*, except around the anchor insertion. The edge of the flat anchor pole forms a delicate undulating crest, further up there are one or two rings of indistinct meshes. Towards the lid narrow impunctate lines form a hexagonal pattern. Despite their small size, all punctures go deep half through the thick chorion. Micropyles below lid, as usual.

Notes. Presumed differences between *O. violaris* and *O. aeripennis* listed by ENDERLEIN (1909) fall within the range of variation of a single species, *aeripennis*, type species of *Ochthopetina* ENDERLEIN, 1909 (by original designation). The large lectotype of *aeripennis* (wings 21 mm) and the smallest syntype of *violaris* (wings 14 mm; only now available and labelled paralectotype, following the action of ZWICK, 1973) each contain a few of the distinctive eggs.

In the collection of F. KLAPÁLEK several specimens (including those listed above, which in turn include those illustrated as *aeripennis* (KLAPÁLEK, 1923, figs. 53–55 on p. 177) are labelled syntypes of “*fusca* KLAPÁLEK”. This is an unavailable nomen nudum published by obvious mistake, and without assignment to a genus (KLAPÁLEK 1923, p. 179). Additional similar specimens in his collection have not been examined in detail; I have not seen the ♂ illustrated as *violaris* (l. c., p. 178), which is certainly also *N. aeripennis*.

The completely black male from Sumatra (wings 16 mm long) is identified with doubt. Penis and T9 are as described, but other details differ a little. T7 is almost simple, the process hardly developed, spinules few. Median sclerite of T8 is narrower, spinules on it less clearly arranged in bands. Anterior process of HT shorter and stouter than usual, posterior outgrowth less developed. This is the only Sumatran specimen known. Whether it is aberrant or represents a separate subspecies or even species is not known.

BANKS (1931) recorded *N. violaris* and *N. aeripennis* from the Malay Peninsula. His material appears to be lost, at least I have been unable to obtain it. I doubt his identifications, because *N. aeripennis* was not among numerous *Neoperla* I have seen from the Malay Peninsula.

I.1.2 *Neoperla caligata* (BURMEISTER) (Figs. 3a–i)

1839 *Perla caligata* BURMEISTER, Handb. Entomol. 2: 880

1923 *Javanita caligata* – KLAPÁLEK, Colls. zool. Baron EDM. SELYS LONGCHAMPS 4/2: 180, fig. 59 on p. 181

Material studied: ♂ neotype (here designated), Java Goenoeng Oengaran, Dec. 1909 (JACOBSON; NMP). Other material: Java: 1 ♂, 2 ♀♀ Tjiandjoer, 8–1000 m V. 1938 (RESSER; ML). 1 ♂, Salak, Warang Loa, Tjionas, 9. XI. 1932; 1 ♂ Buitenzorg Warang Loa, 22. XI. 1931; 1 ♀, Gedeh, Sitroe Goenoeng, 1000 m, 24. IX. 1934 (all LIEF-

* Until respiratory functions are actually proven in Plecoptera I prefer the descriptive term puncture over the recently proposed aeropyle (PICKER, 1980).

TINCK; ML; received as *caligata*); 1 ♀, Radjamandala [= Rajamandala; 6.5 OS/107.20 E] 350 m, 9. V. 1934 (TOXOPENS; ML); 1 ♀, Java occid./Greifsw. (NMP; KAPÁLEK det.: *caligata*). Sumatra: 1 ♀, W. Sumatra, Loeboek Sikaping [PB], 450 m, 1923–27 (HUNDESHAGEN; ML).

Wings of ♂♂ 10.0–10.5 mm, of ♀♀ 11.5–15.0 mm long. Rs forked, anterior branch forked again. Ocelli very small, several diameters apart but not close to compound eyes. Colourful; head, pronotum, wings, appendages (except bases of femora and of cerci) dark brown, remainder yellow. Tentorial calluses and lateral portions of the M-line may appear as paler reddish marks.

♂: Posterior abdominal segments remarkably pilose. Bilobed process of T7 about twice as wide as long. Central sclerite of T8 posteriorly widened, spinules on a posteriorly widened ridge, forming two bands near rear margin. Central sclerite of T9 anterolaterally connected to normal sclerotisation of segment, the usual setose and spinuliferous paramedian swellings behind two transverse crests. Anterior processes of HT massive, plump, distal sections medially flat, parallel to each other. Cerci simple. Sides of S9 with short triangular processes, distal margin with blunt median tip. Penis rectangularly bent, with bare subterminal dorsal protrusion. Penis tube soft, annulate, except on dorsobasal sclerite. At the level of the basal opening the sclerite has a small projecting extension on its outside (compare fig. 4d). The base of the penis rests in the left side of the abdomen. Inner sac simple, little shorter than tube, with uniform armature of many fine spicules, apical ones not distinctly enlarged.

♀: Pilosity of abdomen normal. Bilobed posterior projection of S8 very variable in size and shape, compare figures.

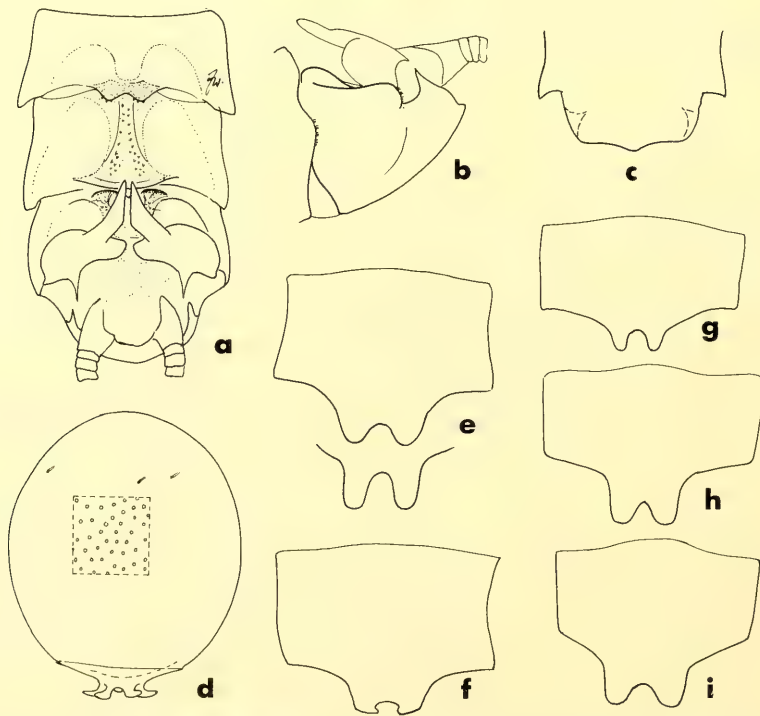


Fig. 3: *Neoperla caligata* (BURMEISTER): Abdominal tip of ♂ (a, b), male subgenital plate from below (c), egg (d; inset size is 0.05 × 0.05 mm) and subgenital plates of ♀♀ of different sizes (given as wing lengths) from various localities: e, Tjiandjoer, both 13 mm; f, Loeboek, 15 mm; g, Radjamandala, 11.5 mm; h, Gedeh, 14 mm; i, Java, KLA-PÁLEK det. *caligata*.

Eggs plump, approx. 0.31 mm long, almost spherical. Narrow collar consisting of 5–6 outwardly bent processes surrounding a small knob to which the anchor (details not known) is attached. Micropyles normal. Chorion irregularly covered by fairly large punctures, except on a polar disc surrounding collar, edge of disc hardly apparent in profile.

Notes: The holotype of *N. caligata* is lost (ZWICK 1972). The beautiful colour figure of it in PICTET (1841) is insufficient for species recognition, several closely similar species are now known to exist. Because the name *caligata* has been used as valid by a number of authors it appears unacceptable to simply abandon its use now. Most authors have followed Klapálek's interpretation of the name, the redescription being accompanied by a good figure. The group of species in question is still insufficiently known. To stabilize the use of the name *caligata*, the ♂ drawn by Klapálek is designated neotype. Sexes have been tentatively associated because in the group they are the most common ones in Java, and have been taken together at Tjiandjoer. Future safe association of sexes and confirmation of *N. caligata* in Sumatra would help definitely establish the specific rank of the closely similar *N. sumatrana*, see below.

N. caligata has been recorded from Thailand and Malaysia (JEWETT 1975). The specimen from Malaysia is no longer available (Dr. PULAWSKI in a letter). The specimens from Thailand were misidentified; they are the same species which has been recorded under the (incorrect) name *N. flaveola* by JEWETT (1975; material has been checked) and also KAWAI (1969; specimen in LFS).

N. laminulata (ENDERLEIN) probably is a junior synonym of *N. caligata*, compare below.

I.1.3 *Neoperla sumatrana* (ENDERLEIN) (Figs. 4a–d, 5a–f)

1909 *Ochthopetina sumatrana* ENDERLEIN, Stett. ent. Ztg. 70: 331, fig. 20.

1966 *Neoperla enderleini* ILLIES, Das Tierreich 82: 270 (unnecessary replacement name).

1973 *Neoperla sumatrana* (ENDERLEIN) (not Klapálek!) – ZWICK, Annls. Zool., Warszawa, 30: 499, figs. 63–65 (lectotype designated).

Material examined: Sumatra: 4 ♂♂, Muara Sako [PB], X. 1915; 1 ♀, Barung Pulau, Kur., VII. 1915 (all JACOBSON; ML). 2 ♀♀, Si-Rambé, XII. 1890–III. 1891 (MODIGLIANI; MCG). 1 ♂, 1 ♀, Wai Lima, Lampongs, XI/XII. 1921 (KARNY; ML). Java: 1 ♀, Mt. Gedeh (Klapálek det.: *laminulata*; NMP). 1 ♀, Java occ., Mons Tjikorai, 4000', 1892 (FRUHSTORFER; Klapálek det.: *javanica* Klapálek; ZMH). 1 ♀, Tjibodas, VII. 1909 (v. D. WHEELER; ML). 1 ♀, Buitenzorg, Tjigoentoer Megamendoeng, 1000 m, 7. VI. 1931; 1 ♀, Gedeh, 1300 m, Tjisaroewa Panggerango, 11. VI. 1932 (both LIEFTINCK; ML); 1 ♀, Tjibodas, TERRY coll. XII. 08. (BPBM).

Slightly larger (wings of ♂♂ 12.0–13.0 mm, of ♀♀ 12.0–20.5 mm long) than *N. caligata*, structurally very similar except, sometimes, large ocelli about one diameter apart. Colouration also similar, but most specimens of *sumatrana* are less contrastive, especially the larger ones sometimes quite pale or dull.

♂: Process of T7 about as long as wide, hardly notched. Bands of spinules on T8 posteriorly confluent. The paramedian swellings of T9 apparent, forming small overhanging lobes. Hemitergal processes bent, much more slender than in *N. caligata*; their tips fit between the lobes of T9. Distal section of S9 set off by lateral notches, lateral appendages very long and slender, blade-like, median point very prominent; there also paramedian angles in the distal margin of S9. Penis similar to the one of *N. caligata* except that apical hooklets of the inner sac are distinctly enlarged. They appear to stand in 3 longitudinal rows.

♀: Similar to *N. caligata*, variable, see figures.

Eggs: Approximately 0.35 mm long, plump oval. Approx. 10 small finger-shaped processes along edge of collar. Details of anchor unknown. Impunctate polar disc surrounding collar difficult to see because the rest of the chorion is covered with club shaped projections standing at the corners of squares or pentagones. Inside each polygone, there are some punctures. Micropyles not observed.

Notes: *N. sumatrana* is so similar to *N. caligata* that I would classify it as its allopatric subspecies, would not females suggest that the sister taxa are sympatric. However, association of sexes requires confirmation. The ♀♀ from Si-Rambé (one of which carried eggs) are completely black like ♂♂ of *N. propinqua* from the same collection. Perhaps they are in fact of that species, but when compared to normally pigmented *N. sumatrana* structural differences have not been observed.

The name *javanica* is an unpublished manuscript name of KLAPÁLEK and is not available. It cannot be excluded that *N. laminulata* is the same as *N. sumatrana*, see below.

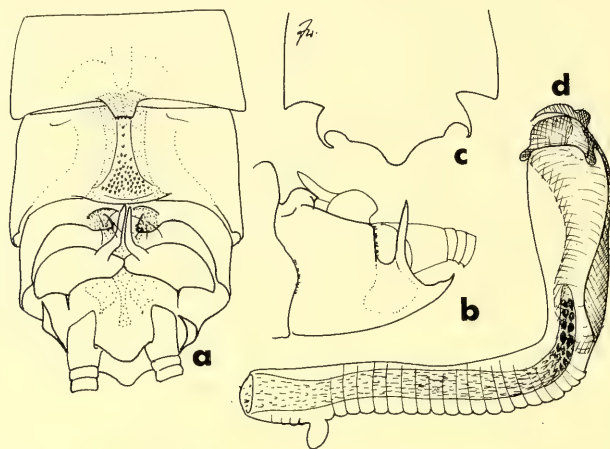


Fig. 4: *Neoperla sumatrana* (ENDERLEIN): Male abdominal tip (a, b), subgenital plate from below (c), penis (d).

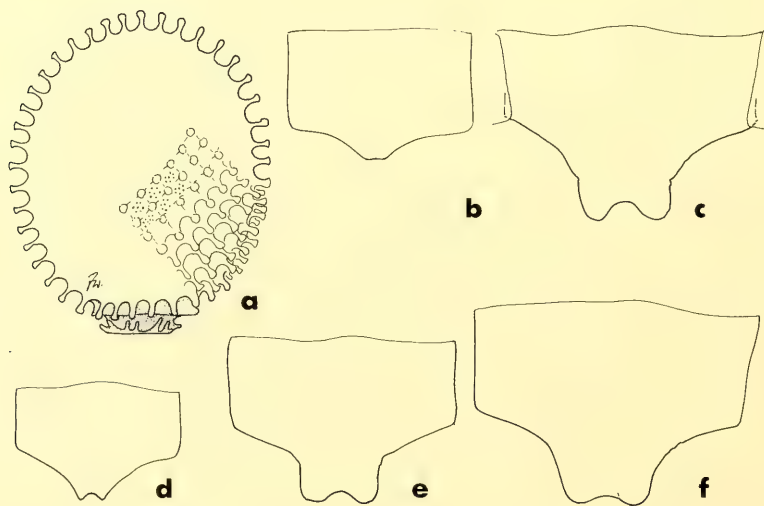


Fig. 5: *Neoperla sumatrana* (ENDERLEIN): Egg (a) and subgenital plates of females of different sizes (given as wing lengths) from various localities: b, Wai Lima, 16.7 mm; c, Java, KLAPÁLEK det. *laminulata*; d, Barnugiulan, 12 mm; e, Tjigoentoer, 16.7 mm; f, Tjisaroea, 20.5 mm.

I.1.4 *Neoperla propinqua* spec. nov. (Figs. 6a–e)

Material studied: ♂ holotype, Sumatra, G. Teleman, V. 1917 (JACOBSON; ML) 2 ♂♂, paratypes, Si-Rambé, XII. 1890–III. 1891 (MODIGLIANI; MCG). 1 ♂, paratype, Simalur, original forest (JACOBSON; ML).

Wings 13–17 mm long. Rs with 2–4, usually 3, branches. Ocelli small, 2–3 diameters apart. Light brown to completely black, except lighter abdomen, reddish tentorial calluses, and M-line on head. The holotype and the specimen from the Island of Simalur have yellow bases of femora.

♂: Process of T7 triangular with rounded tip spinose. Band of spinules on T8 forked only close to end. Swellings of T9 not as distinctly lobe-shaped as in *N. sumatrana*. Anterior process of HT bent, distally tapering. A small sharp granule posteriorly on each HT, opposite basal cercus segment. Sternites simple except S9 which has distinctly angular or even horn-shaped edges and an indistinct median tip.

Penis soft and annulate except on dorsobasal sclerite which has small lateral extensions, almost straight. A subterminal spiny process on the dorsal side is missing in specimens from Si-Rambé. Armature of inner sac consisting of a broad long band of fine spicules dorsally and of a shorter ventral band which is replaced by two rows of larger triangular teeth near the tip.

♀: not known; compare 'Notes' under *N. sumatrana*!

Notes: The amazing variability of several closely similar species makes distinction of taxa in this complex difficult; further study is needed. In the limited material presently available, the combination of elongate triangular lapet of T7, narrow band of spinules on T8, sharp granular process on posterior side of HT, appendages of S9 and the almost straight penis distinguish the present species. Spines on the penial outgrowth (if present) are very exceptional.

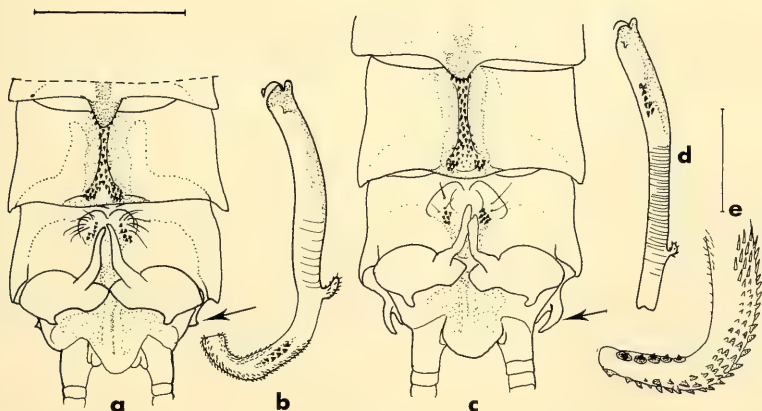


Fig. 6: *Neoperla propinqua* spec. nov.: Abdominal tip of ♂ and penis, with detail of everted inner sac; a, b, holotype; c–e, paratype from Simalur.

I.1.5 *Neoperla aliquia* ZWICK (Figs. 7a–m)

1909 *Ochthopetina sumatrana* ENDERLEIN, Stett. ent. Ztg. 70: 331; in part, not the lectotype on fig. 20!

1923 *Javanita sumatrana* (ENDERLEIN) – Klapálek, Colls. zool. Baron EDM. SELYS LONGCHAMPS 4/2: 182, fig. 61 on p. 183; misidentification.

1973 *Neoperla aliquia* ZWICK, Annls. Zool. Warszawa, 30: 500, figs. 67–69.

Material: Sumatra: 2 ♂♂, 1 ♀, Dolok Ulu, Kora Kora, 15 km NE Pemantang-Siantar, 150 m, 20. IX. 1979 (ERBER; LFS). 1 ♂, 1 ♀, N. Sumatra, I. 1894 (v. D. HOOP; ML); 4 ♂♂, 1 ♀, Balelutu, Alas Valley, 320 m, 3. VIII. 1972, at light in evergreen forest (KRIKKEN; ML); 1 ♂, Mts. Dairi [W of Lake Toba], 2. VI. 1981 (DIEHL; coll. SIVEC). 1 ♀, stream at Balige, Lake Toba, 8. IV. 1929 (THIENEMANN; ML, on slide); 1 ♀, Bangkinan [= Bangki-

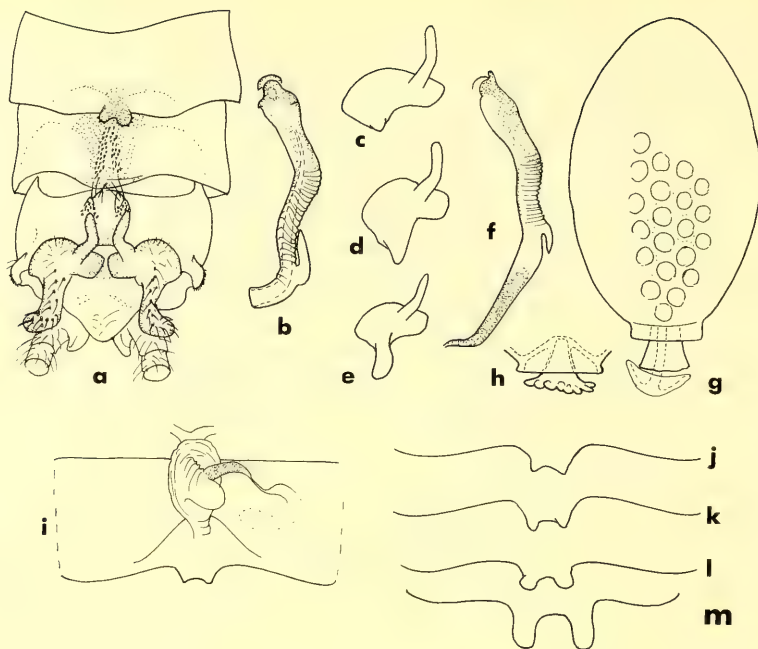


Fig. 7: *Neoperla aliqua* ZWICK: Abdominal tip and penis of ♂ from Andalas (a, b); contour of left hemitergite of specimens from North Sumatra (v. D. HOOP; c), Sandaranagung (d), and from Dolok Ulu (e). f, everted penis of specimen from Balelutu. g, egg from Balelutu. h, anchor pole of an egg from Muara Sako. Subgenital plate of specimens from Wai Lima (i) and Sandaranagung (j-m).

nanag?], June 1937, (BRUES; MCZ). 5 ♂♂, 1 ♀, Muara Sako [PB], X. 1915 (JACOBSON; ML); 2 ♂♂, 4 ♀♀, Sandaran Agung, Kur. Sum., VII/VIII. 1915 (JACOBSON; ML); 1 ♂, Palupuh, V. 1915; 1 ♂, Serapai, VII. 1915; 1 ♂, Tad. Andalas [PB] V. 1914 (all 3 JACOBSON; ML); 1 ♂, Huta Nopan [433 m], Fort de Kock, Sibolga, at light, 20. IV. 1929 (THIENEMANN; ML, on slide); 1 ♀, Padangsidimp[uan] 17. X. 1925, at light (KARNY; ML); 3 ♂♂, Si-Rambé, XII. 1890–III. 1891; 1 ♂, Pangherang-Pisang, XII. 1890 and III. 1891 (all MODIGLIANI; MCG). 4 ♂♂, 7 ♀♀, Wai Lima, Lampongs, XI/XII. 1921 (KARNY and SIEBERS; ML); 2 ♀♀, SW Lampongs, Mt. Tanggamoes, Giesting, 600 and 1000 m, XII. 1934 (LIEFTINCK; ML).

Wings of ♂♂ 12–17, of ♀♀ 16–20 mm long. Rs usually with 3–4 branches. Ocelli moderately large, 1.5 diameters apart, more in ♀♀. Pigmentation variable, from generally ochre to dark brown with brown wings. The pronotum may be brown, or have a median pale band. Bases of femora yellow, tips dark; tibiae either dark or with yellow middle; tarsi dark. Correlations between colour patterns and certain structural variants have not been noticed.

♂: Sternites and cerci simple. Narrow lappet of T7 variable, entire or bilobed, often asymmetrical. The bands of spinules on T8 meet anteriorly. Paramedian setose and spinuliferous lobes of T9 strongly raised, the bent tips of hemitergal processes normally resting between them. The main part of the HT modified, it has an outgrowth opposite the basal cercus segment. It is usually fairly long and straight, tip blunt; often it is very long with plump outwardly curved tip; the ♂ collected by v. D. HOOP in North Sumatra has only a very small swelling.

Penis soft, annulate except at dorsobasal sclerite (which has small lateral extensions), bent at a blunt angle near middle, tip curved ventrally, a bare dorsal subterminal outgrowth (passively moveable, directed either way) present. Inner sac shorter than tube with many spicules, except on a narrow ventral strip. Spicules are fine, largest close to base and in two ventral rows at the apex.

♀: Margin of S8 medially re-entrant and with projecting narrow lobe. The lobe is more or less deeply excised, often asymmetrical.

Eggs: approx. 0.39 mm long, elongate oval, stalk of simple anchor surrounded by narrow long and smooth collar. Edge of smooth polar disc forming a prominent ring so that two collars (a long narrow one inside a short wide one) appear to be present. Chorion outside polar disc covered with large circular depressions between which a hexagonal pattern is faintly visible. Micropyles not observed.

Notes: Colouration, male hemitergites and female subgenital plates vary strikingly but there is practically no overlap with character combinations of related species, so distinction is easy. There appear to be no correlations between particular morphs and colour patterns. Males from a given locality are similar, which may suggest relative isolation of populations. However, all variants of female subgenital plates have been observed within a single sample, compare figs. 7j–m. Sexes appear to be conspecific because they frequently occur together, have larger ocelli than their relatives, and may have banded pronota and tibiae which have not been observed in other members of the group.

I.1.6 *Neoperla rigidipenis* spec. nov. (Figs. 8a–e)

Material studied: ♂ holotype, Sumatra, S. W. Lampongs, top Mt. Tanggamoës, 3.I. 1935 (LIEFTINCK; ML). 1 ♂, paratype, Arr. Saung Ketjil, Sumatra, VIII. 1916 (JACOBSON; ML).

Wings 16.7–17.3 mm long. Rs with several branches, irregular crossveins between these and the anterior branches of M. Ochre, wings fumose, tips of femora and bases of tibiae more or less darkened. Area between ocelli and a median streak leading to anterior margin of frontoclypeus brown; areas in front of ocelli to the sides of the streak also a little infuscate. Pronotum and sides of mesonotum brown, a central yellow dot between the wing bases.

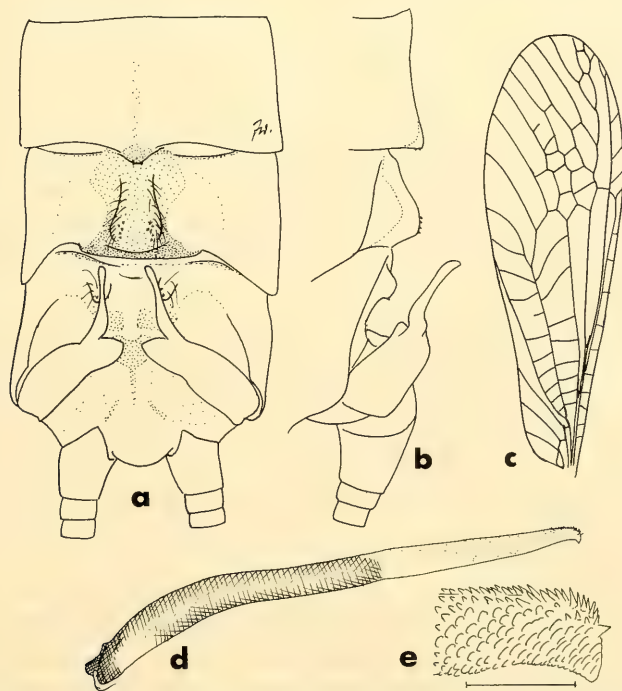


Fig. 8: *Neoperla rigidipenis* spec. nov.: Abdominal tip of ♂ (a, b), front wing (c) and penis with detail of tip of everted inner sac (d, e; scale for e is 0.1 mm).

♂: T7 with very small triangular tip, only 1 or 2 spinules below. T9 with broad median medially constricted sclerite. It carries two sinuous posteriorly diverging swellings beset with long setae on the outside and a few granules medially near end. T9 largely membranous, strongly raised conical setose spiny swellings in front sclerotised. HT slender, strongly transverse, anterior processes long, slender, upcurved, tips slightly thickened. Cerci and sternites simple.

Penis tube completely sclerotised, rigid, 1.8 mm long, distal half narrower than base, slightly curved to ventral side. Internal sac shorter than tube, ventrobasal half bare, rest covered with exceedingly fine triangular spicules, a few larger ones dorsally at the tip. Ventrodistally, spicules are gradually changing to a wider and flatter form and at the apex there are only short transverse scales or crests.

♀: Not known.

Notes: T8 and 9 indicate membership in the *aeripennis*-subgroup. Were the derived member of that subgroup unknown the present species would easily pass as a member of the *clymene*-subgroup. Reticulate venation occurs in all wings of both specimens. In view of the fact that many stonefly species seemingly distinguished by reticulate venation later proved to vary in this respect I am uncertain about its diagnostic value here. Head pattern reminds of the unnamed species As K, L, M, which have no reticulate venation.

I.1.7 Doubtful and unnamed species of the *aeripennis*-subgroup.

Neoperla laminulata (ENDERLEIN)

1909 *Ochthopetina laminulata* ENDERLEIN, Stett. ent. Ztg. 70: 333, fig. 16; type locality: Java.

The form of the subgenital plate suggests that it is either *N. caligata* or *N. sumatrana*. Eggs alone would permit species identification. Unfortunately I have observed none when I redescribed the holotype (ZWICK 1973) and have been unable to obtain it again for study now. A doubtful name.

Neoperla spec. As K (Figs. 9a–e)

Material studied: Sumatra: 1 ♀, Tandj. Andalas, V. 1914; 1 ♀, Balun, Muara Labuh, VII. 1914; 1 ♀, Surian Alahanpandjang, V. 1914 (all Padangse Bovenland; JACOBSON; ML). 1 ♀, Si-Rambé, XII. 1890–III. 1891 (MODIGLIANI; MCG).

Wings 15–25 mm long. Rs with 3 branches. Ocelli small, 2–3 diameters apart. Coloration variable, dull ochre to brownish. In the darkest specimen, head, prothorax and middle of mesonotum are brown; tentorial calluses and M-line appear as pale marks. In the lightest specimen only spot between ocelli and centre of frontoclypeus in front of M-line brownish. Tips of femora, tibiae and tarsi more or less darkened. Wings fumose.

♀: subgenital plate bilobed, internal genitalia typical of the group, not distinctive.

Egg: oval, 0.36 mm long, plump oval. Collar composed of a wide ring of approx. 10 finger-shaped processes, attachment point of anchor (details unknown) flat. Micropyles normal. Area surrounding collar impunctate, very conspicuously separated from rest of chorion by a prominent circular fold. Above this fold, chorion very finely punctate, punctures grouped in polygons separated by very narrow smooth strips.

Notes: Not named because identity with *N. rigidipenis* cannot be excluded.

Neoperla spec. As L (Figs. 9f, g)

Material studied: Sumatra: 1 ♀, Gunung Teleman, V. 1917 (JACOBSON; ML). 2 ♀♀, Mte. Singalang [= G. Singalang], VII. 1878 (BECCARI; MCG). 1 ♀, Balighe [= Balige], X. 1890–III. 1891 (MODIGLIANI; MCG).

Wings 20–22 mm long. Rs with 5 branches, the posterior sometimes originating from anastomosis. Ocelli fairly large, 1.5 diameters apart. Ochre; wings veins, a band from between ocelli to anterior margin of head, antennae (except scape) and tips of tibiae brown.

♀: Distal margin of S8 sclerotised, sinuous, deeply reentrant, with bilobed narrow subgenital plate

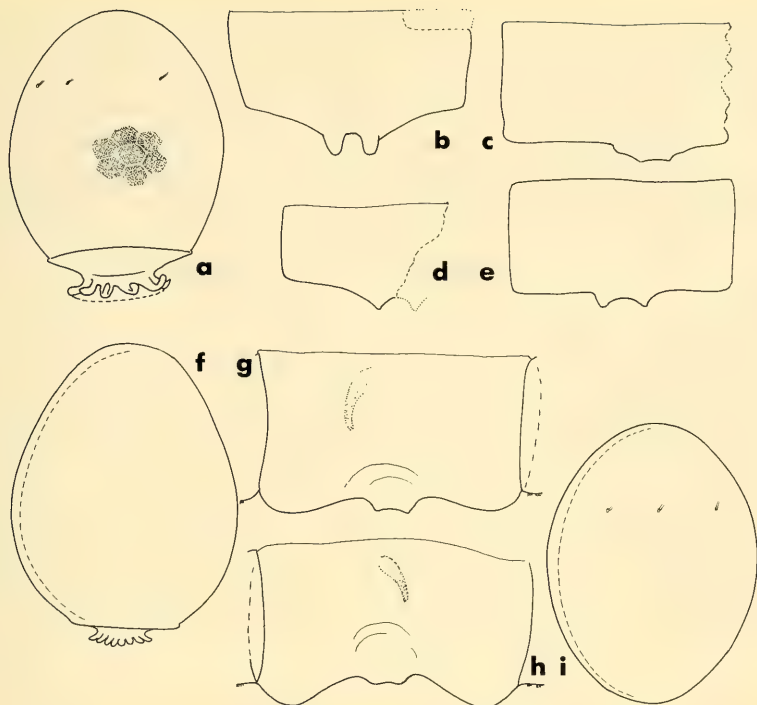


Fig. 9: *Neoperla* ssp.: Eggs and ♀ subgenital plates: a–e, *N. spec. As K* (origin and wing lengths of specimens illustrated: b, Andalas, 16.3 mm; c, Alahan Pandjang; d, Balunpuara; e, Si-Rambé, 25 mm). f, g: *N. spec. As L*. h, i: *N. spec. As M*.

in centre. It is projecting no more than the curved sides of the sternite. A few semicircular folds in front of subgenital plate. Inner genitalia typical of the group, not distinctive.

Egg: Approx. 0.35 mm long, drop shaped, lid narrow, flat anchor pole delimited by circular fold. Collar narrow, its edge extended into ca. 15 short stubs. Anchor present, structure not known. Chorion of uniform thickness, with fine irregular punctation except inside ring surrounding collar. Micropyles not observed.

Notes: Conspecificity with *N. rigidipenis* cannot be excluded, the species is therefore not formally named.

Neoperla spec. As M (Figs. 9h, i)

Material studied: 1 ♀, Sumatra, Gunung Teleman, VI. 1917 (JACOBSON; ML).

Wings 18 mm long. Similar to *N. spec. As L*, except completely infuscate tibiae, and egg.

Egg: regularly oval, both poles similar, collar and anchor absent. Chorion much thinner at poles than near equator of egg. Appears smooth but is in fact finely and irregularly punctate. Micropyles normal.

Notes: The species is not named because it might be the ♀ of *N. rigidipenis*.

I.2 The *clymene*-group s. str.

Males are very diverse and share no common diagnostic character, except being unlike the former. Females may or may not have subgenital plates. Their receptacular stalks are distinctive. They are wide, internally armed with spicules, spirally coiled, usually very long. Often, 1 or several complete rings are

formed by the coiled stalk to which the receptacle is directly attached. Egg sculpture is varied. Irregular punctation between few longitudinal ridges and small meshes on collar and lid appear to be the primitive condition. In derived species, bare ridges are numerous, sulci between them become narrow. When sulci are very narrow, irregular punctation is replaced by two regular rows of punctures, one on each side of the sulcus. Every sulcus is connected to a single mesh on the collar and/or lid.

This subgroup includes all American species described by STARK & BAUMANN (1978; groups defined by them are subunits within the *clymene*-subgroup, some probably artificial), all African species known to me, and many Asian species, e. g. the group of species around *N. katmanduana* HARPER (ZWICK & SIVĚC 1980). No further subdivision of the subgroup is presently attempted.

I.2.1 *Neoperla primitiva* GEIJSKES (Figs. 10a–g).

1909 *Neoperla sumatrana* Klapálek, Wien ent. Ztg. 28: 220 (not *N. sumatrana* [ENDERLEIN, 1909], not *N. sumatrana* of Klapálek, 1923 [misidentification]).

1952 *Neoperla primitiva* GEIJSKES, Arch. Hydrobiol., Suppl. 21: 292, fig. 8.

1973 *Neoperla inutilis* Zwick, Anns. Zool. Warszawa, 30: 499 (replacement name for *N. sumatrana* Klapálek, nec ENDERLEIN); = *N. primitiva inutilis*, stat. nov.

Material examined: *N. primitiva primitiva*: ♂ holotype, Sumatra, Muara Klingi am Musi, at light (FEUERBORN; ML; on two slides). Additional material: Sumatra: 1 ♂, Tamiai, Kur., VII. 1915 (JACOBSON; ML). Alas Valley: Kutatjane, Tanah-Merah, 200 m, native gardens, at light: 5 ♂♂, 1 ♀, 4.–8. VI. 1972; 1 ♂, 1 ♀, 9. VIII. 1972; Balelutu, evergreen forest, 3.–8. VIII. 1972 (all KRIKKEN; ML). 6 ♂♂, 8 ♀♀, Pasar Manduge, 20 km SE Pematangsiantar, 200 m, original forest, at light, 30. VIII. 1979; 1 ♀, Dolok Ulu, Kora Kora, 15 km NE Pematangsiantar, 150 m, at

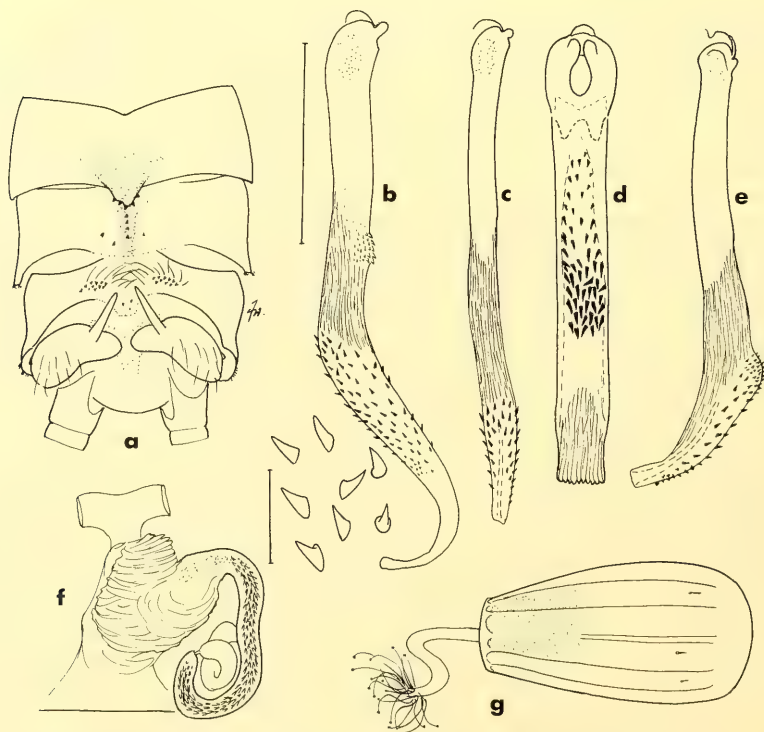


Fig. 10: *Neoperla primitiva* GEIJSKES; Abdominal tip of male (a), penis (b–e), vagina (f) and egg (g). Figs. a, b, f and g are of *N. primitiva primitiva*, c, d of *N. primitiva inutilis* Zwick, e of the holotype of *N. primitiva separanda* ssp. nov.

light, 20. IX. 1979 (all ERBER; LFS). – *N. primitiva inutilis*: ♂ holotype, ♀ paratype (at the same time, lecto- and paralectotype, respectively, of *N. sumatrana* KLAPÁLEK, here designated), Sumatra, Cotypus, Berlin (Coll. KLA-PÁLEK; NMP). Additional material: Sumatra: 2 ♂♂, 3 ♀♀ Morea Mahat [Muaramahat, = 16 N/100.49 E]; 1 ♂, 1 ♀, Bankinan [= Bangkinang?]; 5 ♀♀, Pematangsiantar (all June 1937, BRUES; MCZ). 2 ♂♂, 1 ♀, E. coast, Langkat [= 40 N/98.10 E], Namo Dengas Estate [Deli], 26.–29. XI. (JOURIN; MCZ; BANKS det.: *jacobsoni*). Java: Buitenzorg, 1 ♂, IV. 1908; 1 ♂, 30. XI. 1930, at light (LIEFTINCK; ML). – *N. primitiva separanda* ssp. nov.: ♂ holotype, Java, Djasinga, 25. XI. 1912 (ML). – Single ♀♀ not assigned to subspecies: Sumatra: 1 ♀, Serdang District, Bandar Kwala Estate (PUTTFARCKEN dedit 1. X. 1894; ZMH; KLAPÁLEK det.: *fallax*!). LOMBOK: 1 ♀, Swela, 22. III. 1927 (RENSCH; ZMB).

N. primitiva appears to be a polytypic species where males differ in details of the penis. However, the forms distinguished are not all vicariant. It may be, that ssp. *primitiva* and ssp. *inutilis* will later prove to be the same, because some ♂♂ of the latter in MCZ have single teeth on the outside of the penis; possibly more clearly intermediate specimens do exist. Females appear to be all similar.

Wings of ♂♂ 9–10, of ♀♀ 10–12 mm long. Rs forked once at or near anastomosis. Ocelli large about 1.5 diameters apart, slightly more in ♀♀. Yellow to ochre; antennal flagellum, palpi, dorsal streak on femur, tibia, tarsus, distal half of cercus und spot between ocelli darker than rest, sometimes dark brown. In the darkest specimen (from Pasar Manduge) the cephalic mark extends sideways behind the occipital suture, while the area in front of the suture is bright yellow. The same specimen has a brown mark in front of the M-line.

♂: Extension of T7 triangular, often asymmetrical, granules along its sides and below. Median sclerite of T8 very narrow, band shaped, a single line of spinules on it, occasional spinules to its sides on the membrane. T9 normal, with paramedian raised areas. HT simple, anterior process pointed, straight, very short. Sternites and cerci simple.

Penis straight, tubular, long; it occupies the last three abdominal segments. Distal surface of tube and base of inner sac with fine longitudinal striation. Armature of inner sac consists of irregularly placed very slender and quite large teeth, those near base of sac are largest. The subspecies differ as follows:

N. primitiva primitiva: A dorsodistal patch of little spines externally on penis tube, most basal teeth on inverted sac in immediate vicinity of these outer spines. Everted sac gently S-curved, basal portion gently curved to dorsal side.

N. primitiva inutilis: penis narrower than in nominate form, no external spines (or only single ones present), striate section longer. Most basal teeth on inverted sac situated far from tip near middle of penis tube. Everted sac straight.

N. primitiva separanda ssp. nov.: Penis tube slender without external spines. Striate section short on dorsal, long on ventral side. Internal sac bent to ventral side. Teeth on everted sac occur only on dorsal side, the most basal ones small, assembled on a small protrusion.

♀: No external modifications. Vagina typical of the group. Receptacular stalk about as long as 8th segment, forming a half circle. Near base, the stalk contains numerous fine spinules which become larger and stouter towards tip of stalk; spinules in its distal half are exceptionally large and plump.

Eggs about 0.28 mm long, elongate, lid distinctly wider than anchor pole. No collar. Anchor inserts in centre of flat pole, its stalk being more than half as long as the entire egg. It carries a flimsy small disc with marginal granules resembling the usual mushroom-shaped anchor. However, in most eggs the disc is disintegrated into numerous delicate threads, each with a granule at its tip. Sides of egg with approx. 15 straight broad impunctate ribs. Wide sulci irregularly punctate. Micropyles occur singly in sulci close to lid.

Notes: GEIJSKES' (1952) description and figure are excellent but the distinctive penis was not described. It is clearly visible inside the mounted holotype. The record of *N. primitiva* from India (KAWAI 1969) was based on a specimen of which fragments are preserved in LFS; the penis is missing. Although specific identification is no longer possible it is clearly not the present species.

The name of the taxon has a confused history. For a long time, *N. sumatrana* KLAPÁLEK was considered to be valid. Nobody appears to have noticed that the species originally described (KLAPÁLEK 1909) is very different from the one to which the name was later applied (KLAPÁLEK 1923; see *N. distincta*!). When *Ochthopetina* and other nomi-

nal genera of *Neoperlini* were synonymised with *Neoperla* (HYNES 1952) a case of secondary homonymy between *N. sumatrana* KLAPÁLEK, 1909 and *N. sumatrana* (ENDERLEIN, 1909) arose. ILLIES (1966) was in error when he replaced ENDERLEIN's name: it had been published several months before KLAPÁLEK's which needed replacement. If distinctness of ssp. *inutilis* from the nominate form should in future be confirmed creation of the replacement name *inutilis* would not have been as useless as I thought it was.

1.2.2 *Neoperla jacobsoni* KLAPÁLEK (Figs. 11a–c)

1910 *Neoperla jacobsoni* KLAPÁLEK, Notes Leyden Mus. 32: 38, fig. 3.

Material studied: 1 ♂ lectotype, 1 ♂ paralectotype, Java, Semarang, VI. 1909 (JACOBSON); 1 ♂ paralectotype, Java or., Ardjoeno (HEKMEYER; lectotypes here designated, all NMP). Additional material: Java: 1 ♂, 1896; 1 ♀, III. 1910; 1 ♀, X. 1910, specimen incorrectly labelled syntype of *N. dolichocephala* KLAPÁLEK (JACOBSON; NMP). 1 ♀, Buitenzorg, 30. III. 1930, at light (LIEFTINCK; ML). Sumatra: 1 ♂, Soerak [?], IV. 1878 (Sumatra-Exped.; NMP); 1 ♀, Sumatra (LEBER; ZMB, Journal Nr. 67/1913). 1 ♀, Pad [agnse] Bovenl [and], IV. 1914; 1 ♀, Kloof van Anai [= Lembah Anai, 0.50 S/100.17 E], III. 1915 (both JACOBSON; ML).

Wings of ♂♂ 9–10, of ♀♀ 11–13 mm long. Rs with 3 branches, posterior usually from anastomosis. Yellow; ocellar rings or a small mark connecting ocelli brown. Antennae (except scape and pedicel) and tarsi dark, sometimes also tibiae infusate.

♂: Externally similar to *N. primitiva*. Penis elongate, widened towards apex, rather soft, with transverse folds dorsally in distal half. Most of penis tube covered with small asperities. Inner sac narrow, coiled to ventral side. It is largely bare, except a group of very fine spicules dorso-basally and two rows of quite large hooks in the middle on the concave (= ventral) face of the everted sac.

♀: No external modifications. Vagina normal, modified stalk of receptacle forming an almost complete circle internally lined with many small sclerotised scales.

Egg 0.30 mm long, oval, collar well developed. Anchor apparently normal, attached in a deep depression of chorion. A single row of meshes on collar. Chorion densely striate above these, bare ridges

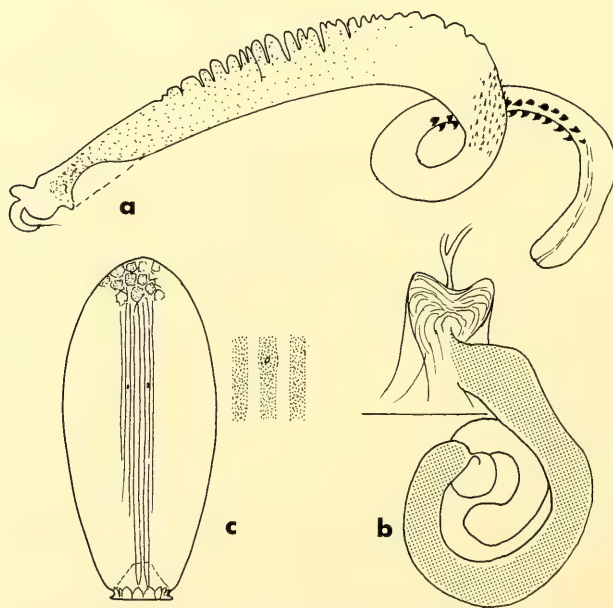


Fig. 11: *Neoperla jacobsoni* KLAPÁLEK: Everted penis (a), vagina (b; to same scale as penis) and egg (c) with detail of sculpture.

not much narrower than irregularly punctate sulci. Micropyles singly in sulci, closer to middle of egg than to punctate and reticulate lid.

Notes: The syntype from Soeroelangoeng, Sumatra, was not located; the fragment from Muki (KLAPÁLEK 1923) can no longer be identified. Several additional specimens which were incorrectly labelled syntypes of *N. jacobsoni* in coll. KLAPÁLEK have not been examined, their identity is doubtful. The transverse folds on the penis remind of the *aeripennis*-group but this is probably only a superficial resemblance, external characters being typical of the *clymene*-group s. str. Common occurrence of both sexes at Samarang and existence in Sumatra as well as Java support association of sexes. Note the good agreement in size of everted penis sac and receptacular stalk. Compare *N. spec. As J!*

I.2.3 *Neoperla vesperi* spec. nov. (Figs. 12a–c).

Material studied: ♂ holotype, Sumatra, Pasar Manduge, original forest 10 km SE Pematangsiantar, 200 m, 30. VIII. 1979, at light (ERBER; coll. ZWICK). ♀ paratype, Dolok Ulu, Kora Kora, 15 km NE Pematangsiantar, 150 m, at light, 20. IX. 1979 (ERBER; coll. ZWICK). 1 ♀ paratype, Tandj. Andalas [PB], V. 1914 (JACOBSON; ML).

Wings of ♂♂ 10, of ♀♀ 12 mm long. Rs with 3, in one wing with 4 branches, the posterior at or close to anastomosis. Ochre, wings distinctly infusate. Legs dark except bases and tips of femora and tips of tibiae. Centre of head yellow, peripheral areas along eyes, antennal sclerite and M-line ochre. A dark band immediately behind occipital suture and a spot between ocelli brown, posterior portion of occiput bright yellow. Palpi, scape and pedicel brown, flaggellum black. Cerci incomplete, apparently dark except base.

♂: External genitalia generally similar to *N. primitiva* and *N. jacobsoni*. T8 with triangular central sclerite with irregular spinules. Strong swellings of T9 with setae and spinules, some extra spinules in depressed centre. Hemitergal processes plump, blunt, almost straight. Posterior face of hemitergites beset with long brown setae, otherwise simple. Sternites and cerci simple.

Penis 1 mm long, tubular with band shaped ill defined dark dorsal and ventral sclerites. Much of outside covered with minute asperities taking the shape of minute teeth at the end of the dorsal sclerite. Tip of tube bent to ventral side beyond end of dorsal sclerite, a few basally directed spinules at bend, a sparse group of fine pale teeth dorsally and on sides near tip. Internal sac very long and narrow undulating inside penis tube. At some distance from base with many small fine teeth, the straight distal section

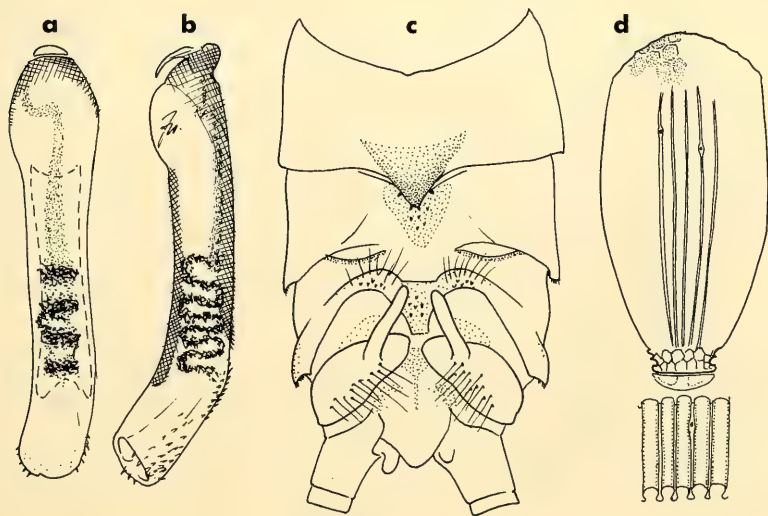


Fig. 12: *Neoperla vesperi* spec. nov.: Penis (a, b), abdominal tip of ♂ (c), egg, with detail of chorion sculpture (d).

has a denser cover of still finer teeth. Artificial eversion was only partly achieved, the sac is apparently straight, the triangular teeth have no apparant order except being sparse laterally.

♀: Centre of S8 more strongly pigmented than rest, brownish. Internal genitalia similar to *N. jacobsoni*. Distinction will have to rely on colour pattern and mainly on eggs.

Eggs 0.33 mm long, elongate drop shaped, collar narrower than lid. Collar with 2 rows of meshes, lid with punctate polygonal meshes, remainder of chorion densely striate. Bare ribs much wider than narrow depressions. Each depression with 2 regular lines of punctures which are not interrupted in places where micropyles occur. Sides of ribs bulge over depressions, in slide mounts punctures therefore appear to be on ribs. Anchor mushroom-shaped, simple.

Notes: The distinct pattern of specimens from near Pematang Siantar was used for tentative association of sexes. An evident relative of *N. jacobsoni* and *N. inutilis*, but penis and also external genitalia distinct. The *Neoperla* taken near Pematang-Siantar by D. ERBER all came to light only between 19⁰⁰ and 21⁰⁰ hours. The name of the present species refers to its evening activity.

I.2.4 *Neoperla distincta* spec. nov. (Figs. 13a-c).

1923 *Neoperla sumatrana* – Klapálek, Colls. zool. Baron EDM. SELYS LONGCHAMPS 4 (2): 145, fig. 17 on same page (misidentification; not *sumatrana* Klapálek, 1909; not *sumatrana* Enderlein, 1909!).

Material studied: ♂ holotype, Sumatra, Distr. Serdang, Banda Kwala Estate (PUTTFARCKEN dedit 1894; ZMH; Klapálek det. *sumatrana* Klap.) Malaya: 1 ♂, paratype, Pahang, Kuala Tahan, 15.–16. XII. 1958 (QUATE; BPBM). Thailand: 3 ♂♂, paratypes, Krachong Forest near Trang, 100 m, 2. VII. 1962 (ROSS & CAVAGNARO; JEWETT det. 1969: *N. nitida* KIMMINS; CAS, LFS). 3 ♂♂, paratypes, Trang Prov. Khaophappa, Khaochang, 200–400 m, 31. XII. 1963–15. III. 1964 (SAMUELSON; BPBM); 2 ♂♂, paratypes, Banna Chawang nr. Nabon, 70 m, 5. IX. 1958 (GRESSITT; BPBM, LFS).

Wings of ♂♂ 7.5 mm long. Rs simply forked. Eyes very large and prominent. Pale yellow, rings surrounding ocelli and distal portion of antennae dark.

♂: Projection of T7 broadly rounded at tip. On T8, indistinct elongate sclerite beset with few spinules in its anterior half. T9 with usual paramedian swellings and bare median depression. Hemitergites exceptional, appearing to be bent at right angle because of a posteromedian broad extension. Pale setae are forming a silky fringe along its mesodistal edge. Anterior process of HT normal, slender and gently curved. Sternites and cerci simple.

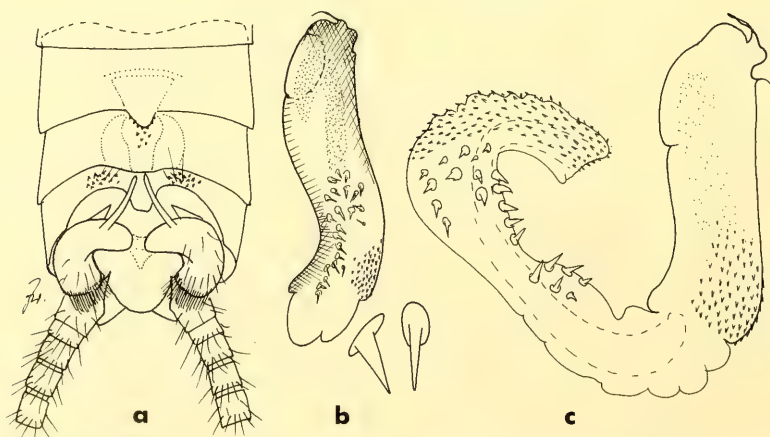


Fig. 13: *Neoperla distincta* spec. nov.: Abdominal tip of ♂ (a), contracted and everted penis, with detail of major hooks (b, c).

Penis about 1 mm long, a gently S-shaped tube particularly strongly sclerotized dorsally near base and ventrally near tip. A large group of external spinules occupies the ventral and lateral sides of the tip. Laterally, they are connected to the usual patch of fine ventrobasal asperities. The inverted sac appears as a number of very slender and exceptionally large spicules in distal half, and as a dense band of fine triangular spicules basally. Everted sac first curved ventrobasally and then recurved towards penis tube. Wide base of sac bare. Big spines first appear ventrally, and then spread across the sac. Distally they are replaced by numerous small triangular spicules which leave the ventral side of sac bare. Uneverted distal half of sac is largely bare, wide, strongly folded; it is doubtful whether it is ever fully everted.

♀: not known.

Notes: Klapálek introduced the name *sumatrana* for a species with pointed process of tergite 7 and simple hemitergites 10. His description agrees with syntypes in his collection. In the posthumous redescription of *N. sumatrana* Klap. (Klapálek 1923) arranged by Šámal, the name is erroneously applied to a different species; the figure had been prepared from the holotype of the present *N. distincta*. Real *N. sumatrana* Klap. later became a junior secondary homonym of *N. sumatrana* (Enderlein) and had to change name; see *N. primitiva inutilis*!

1.3 Unnamed species of the *clymene*-group s. str.

Neoperla spec. As J

Material studied: Sumatra: 1 ♀, Distr. Serdang, Bandar-Kwala-Estate (Puttfarcken dedit 1894; ZMH; Klapálek det.: *sumatrana* Klapálek). 1 ♀, Nitahon, 21. V. 1961 (Diehl; coll. Sivec). 1 ♀, Dolok Merangir, 10.–14. VI. 1981 (Diehl; coll. Sivec). Malakka: 1 ♀, Camp Jor, Wasserscheide zwischen Perak und Pahang (Grubaer leg. et vend. 1902; ZMH; Klapálek det. *Neoperla* spec.).

Wings 12.5–14.0 mm long, venation like in *N. jacobsoni* which is also similar in colouration and ♀ genitalia. The eggs of the present species differ from those of *N. jacobsoni* by slightly narrower collar and especially by distinctly flanged ribs, most apparent on reticulate lid.

Notes: The species is not formally named because the male is unknown and conspecificity with *N. jacobsoni* is not completely excluded. Although the ♂ type of *N. distincta* from Bandar-Kwala-Estate and the female from the same locality have together been (mis-)identified as *N. sumatrana* Klapálek by Klapálek they are certainly not conspecific in view of their very different sizes and the different venation.

II. The *montivaga*-group

External genitalia of males in this group are variable, but T9 seems never to be strongly raised or remarkably modified in other ways. Penis variable, usually wide and plump. Its sclerotisation is restricted to a dorsal sclerite surrounding the basal opening and then tapering distally, and to a short ventromedian sclerite connected to the basal one. Instead of the smooth ventral edge of the sclerite basally from the soft area observed in the *clymene*-group, a sclerotised band extends ventrally over the basal forth of the penis.

The vagina is very large and wide, strongly folded. It may be modified and armed in a variety of ways. In all cases, the receptacular stalk is unmodified, short, thin, simple.

Eggs are variously shaped and sculptured. If the chorion is striate, punctation of sulci may be irregular, like in primitive members of the *clymene*-subgroup. In the more advanced members of the *montivaga*-group, every sulcus contains only a single series of punctures. Three narrow sulci are connected to every single mesh on the collar or lid if these are reticulate.

Adult diagnostic characters of the *montivaga*-group are clearly plesiomorphic: The arrangement of penis sclerites is the same as in *Phanoperla* and *Chinoperla*, and their simple female genitalia are also

generally similar. Still, at least species with uniserial punctation of eggs probably form a monophyletic unit. Other characters permit delimitation of small sets of closely related species some of which have this particular chorion structure while others have irregularly sculptured or smooth eggs. The egg character by itself is apparently not sufficiently diagnostic and liable to secondary modifications. It may therefore be that the *montivaga*-group as here defined includes also some species which happen to be similarly primitive in the key characters but belong to different evolutionary lines.

A satisfactory general subdivision of the *montivaga*-group is not yet possible. Recognizable subunits are evidently of subordinate rank and not comparable to the major subgroups of the *chymene*-group defined above. Most species treated here are close relatives of *N. luteola* and only this subgroup is defined. The remaining members of the *montivaga*-group from Sumatra and Java are described and listed without assignment to a particular subgroup.

II.1 *The luteola*-subgroup

Males have a broad rounded extension of T7, and a very wide ill defined sclerite on T8. T9 is normal, medially depressed, with groups of paramedian setae in front and groups of spinules behind these. Hemitergites with bent anterior processes. Brushes of setae on male sternites 7 or 8 are distinctive. The seminal receptacle appears to insert far posteriorly because it is attached to the overhanging tip of a cone formed by the vagina. Eggs irregularly sculptured, or smooth, or densely striate with uniserial punctation in sulci.

Presence of sternal brushes on posterior abdominal segments is the distinctive character of this subgroup which is only known from the Sunda Islands. It is a primitive trait but additional similarities between included species indicate that they are in fact close relatives. However, presence of sternal brushes (on sternites 3–5 in this case) cannot be used to show that the south Indian *Neoperla nitida* KIMMINS is a member or relative of the *luteola*-subgroup. Details of penis armature, vagina, and eggs (ZWICK 1981) of *N. nitida* would fit well into the grouping proposed here.

II.1.1 *Neoperla luteola* (BURMEISTER) (Figs. 14a–d)

1839 *Perla luteola* BURMEISTER, Handbuch der Ent. 2: 881.

1972 *Neoperla luteola* – ZWICK, Rev. suisse de Zool. 78 (1971): 1176, Abb. 10a, b (lectotype).

Material studied: Java: 1 ♂, Buitenzorg, at light, 28. XII. 1929; 1 ♂, W. Java, Palaboean ratoe, Tjisolok, 1. V. 1932 (LIEFTINCK; ML). 1 ♂, Buitenzorg, III. 09; 1 ♂, Bantar Gebang [= Bantargebang, either 6.17 S/106.58 E or 7.01 S/106.40 E] (both BRYANT & PALMER; MCZ; BANKS det.: *flaveola* KLAP.). 1 ♀, Central Java, Mendut [7.36 S/110.13 E], 2. IV. 1981 (DE ROUGEMONT; my coll.). 1 ♂, Bali, Ubud, 29. XI. 1975 (MONTEITH; University of Queensland).

Wings 10–13 mm long. Rs with simple fork. Ochre, no distinct pattern. Ocelli large, about one diameter apart.

♂: External genitalia and general shape of penis typical of subgroup, not distinctive. Penis armature consists of very many small stout teeth without apparent order when inner sac is retracted. At its base, there are two small spiny outgrowths which are distinctive. The everted sac forms an almost complete ring on the ventral side of the penis. Along the concave inner face of the ring teeth are minute, the ones on the outside distinctly larger, less so in apical third of sac.

♀: No external modifications. Vagina forms a long central cone with very many strong circular folds in front. Two small rough sclerites on its rear side largely covered by overhanging tip of cone which carries the receptacle.

Eggs oval, approx. 0.34 mm long, collar wide and very short, not prominent, anchor simple. Chorion with many longitudinal rows of small punctures in deep very narrow sulci; smooth raised portions between sulci about four times wider than a sulcus. Sulci originate in groups of three at collar and end in groups of three below punctate polygons covering blunt lid. Compare figures of eggs of *N. pilosella*, which are completely similar.

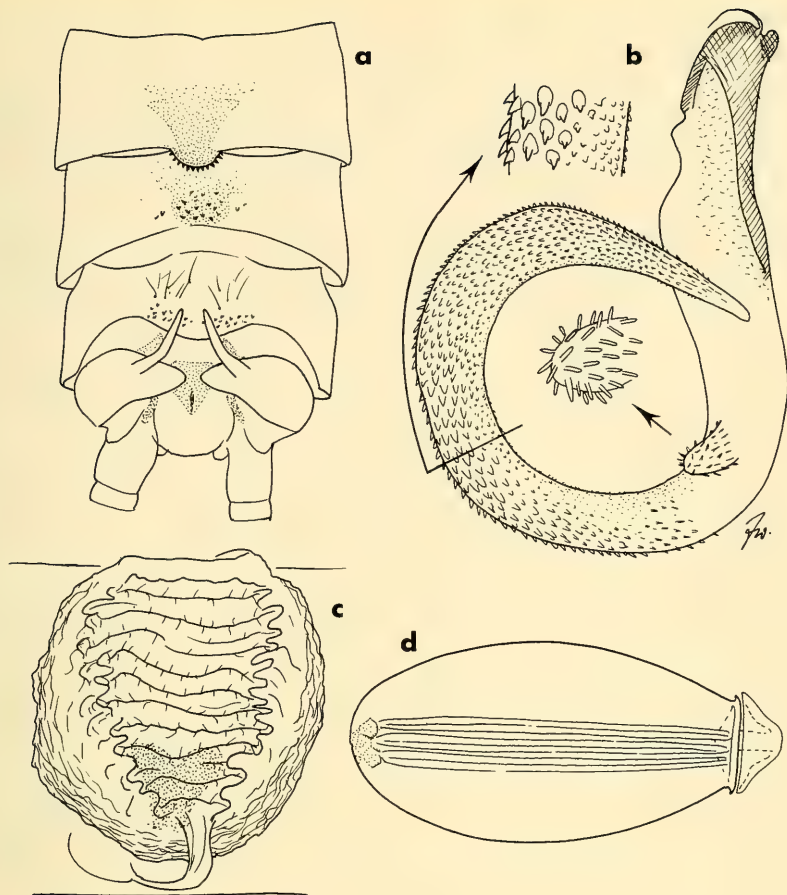


Fig. 14: *Neoperla luteola* BURMEISTER: Abdominal tip of ♂ (a), everted penis with details of armature (b), vagina (c) and egg (d).

Notes: When the penis sac is completely retracted so that the basal outgrowths are not visible, *N. luteola* is best recognized by seemingly uniform dense and fine armature, and by absence of small spines on outside of penis tube. The vagina is very similar to the one of *N. simplicior* which, however, is a little shorter and lacks posterior rough sclerites; eggs of *N. simplicior* are very different. Eggs of *N. luteola* and *N. affinis* cannot be distinguished, but female genitalia of the two differ clearly.

Males of *N. luteola* and females described above were the only members of the subgroup in Java with the other sex unknown. Their association is supported by great similarity, in male and female genitalia, to *N. simplicior* NAVÁS.

N. luteola has been thought to be a senior synonym of *N. pilosella* and *N. rubens* (ENDERLEIN 1909; GEIJSKES 1937, 1952; ILLIES 1966) but this is not so, see *N. pilosella*. *N. luteola* is a rare species unknown in Sumatra, specimens listed here and in ZWICK (1972) are all known. I cannot confirm additional records from Java and Sumatra (BANKS 1931; ENDERLEIN 1909; GEIJSKES 1937, 1952; KLAPÁLEK 1909, 1910, 1912, 1923), at least some of which were based on misidentified specimens (see *N. pilosella*, *N. simplicior*, *N. fallax*). Specimens from Tonkin (NAVÁS 1930; in MNHNP) belong to several misidentified species and I believe that material from the Malay Peninsula and Borneo (BANKS 1931, NAVÁS 1929) that I have not seen had also been misidentified. At any rate, no *N. luteola* were among the numerous specimens from Borneo and the Malay Peninsula I have seen. Malayan *N. luteola* recorded by BISHOP (1973; specimens in LFS) are in fact *N. fallax*.

II.1.2 *Neoperla simplicior* NAVÁS (figs. 15a–d)

1932 *Neoperla simplicior* NAVÁS, Mem. Pont. Accad. Sci. nuov. Lincei (2) 16: 953, fig. 66.

Material studied: ♂ holotype, Sumatra, Pangherang-Pisang, X. 1890–III. 1891 (MODIGLIANI; MCG). Additional material: Sumatra: 2 ♀♀, Langkat [3.40 N/98.10 E], Namoe Dengas Estate, 25. XI. (JOURIN; MCZ; BANKS det.: *N. jacobsoni*). 1 ♂, Pematangsiantar, June 1937; 2 ♀♀, Bangkinan [= Bankinang ?], June 1937 (all BRUES; MCZ). 1 ♂, NO Sumatra, Tinggi Radja, Deli, 9. XI. 1928 (V. D. MEER MOHR; ML). Nitahoan, 20. V. 1981 (DIEHL; coll. SIVEC). 6 ♂♂, 5 ♀♀, Dolok Ulu, Kora Kora, 15 km NE Pematangsiantar, 150 m, at light, 20. IX. 1979 (ERBER; LFS). Alas Valley, Kutatjane, Tanah Merah, 200 m, 1 ♂, 4.–8. VI. 1972, 2 ♂♂, 9. VIII. 1972; 1 ♀, Alas Valley, Balelutu, 320 m, 3.–8. VIII. 1972 (all KRIKKEN; ML). 1 ♂, 1 ♀, Balun, Pad. Bov., VI. 1914; 1 ♀, Muara Jabu, VII. 1914; 1 ♂, I. 1914, 1 ♂ (SAMAL det.: *luteola*), I. 1921, Fort de Kock; 1 ♂, Tanangtalu [PB], V. 1915 (all JACOBSON; ML). 1 ♂, Padangsidimpuan, 18. X. 1925 (FULMECK & KARNY; ML). Identified with doubts: 1 ♀, Sumatra (OVERSTREET; BPBM).

Wings of ♂♂ 10–11, of ♀♀ 11–12 mm long. Rs with simple fork. Ocelli large, close together. Yellow, ocellar rings, antennae except base, tips of cerci, tarsi, usually tibiae, rarely also tips of femora dark.

♂: Similar to *N. luteola* except penis. Penis plump; everted inner sac forms an almost complete ring on ventral side of tube. Its distal tip covered with fine fairly uniform small teeth. A broad bare strip on convex (= dorsal) $\frac{3}{4}$ of everted sac flanked by very large curved hooks. This band in turn accompanied by a band of very slender, fine spinules; basal half of concave face bare.

♀: No external modifications. Vagina membraneous except thin sclerotized loop surrounding distal part of common oviduct. Dorsal face of vagina forms regular parallel folds in front and a raised central cone to the tip of which the receptacle is attached. Posterior half of vagina below raised cone very delicate, irregularly folded and wrinkled, evidently very extensible.

Eggs approx. 0.26 mm long, regularly oval, collar a narrow very short ring. Simple mushroom shaped anchor inserts in a depression. Surface seemingly smooth, covered by very dense and fine irregular punctuation except on collar. Micropyles in upper third of egg.

Notes: NAVÁS' figure resembles a *Phanoperla* because the process of T7 is not shown, details of T8 and T9 are not visible, shape and position of hemitergites 10 are incorrect. Long delicate basolateral spines and large hooks scattered.

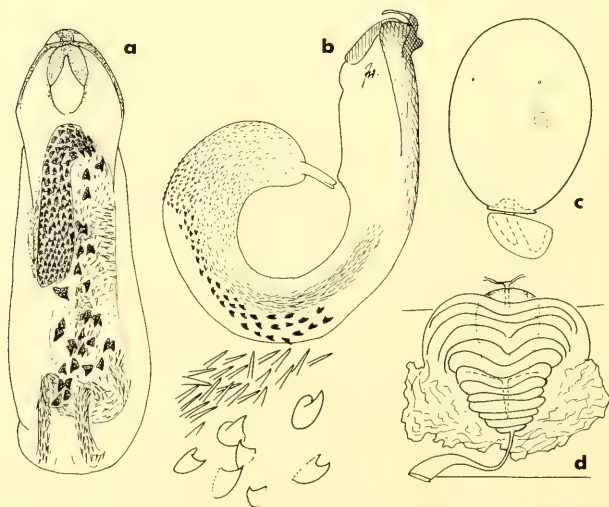


Fig. 15: *Neoperla simplicior* NAVÁS: Penis in resting (a) and everted condition, with details of armature (b), egg (c) and vagina (d).

red over a wide stretch are visible already in contracted penes and easily distinguish *N. simplicior* from its close relatives. Other females in this group have generally similar vaginae, but all have at least some sclerotisation of the anterior folds, or of the surface behind these. Eggs are somewhat similar to those of *N. caligata* but differ by finer punctation and differently shaped collar. Association of sexes is based on repeated common occurrence, and the fact that at Dolok Ulu they were the only common species in the sample. Eggs of the doubtful ♀ in the Bishop Museum have a slightly more developed collar and their dense punctation is arranged in longitudinal lines, but there is no striation.

II.1.3 *Neoperla fallax* Klapálek (Figs. 16a–i)

1909 *Neoperla fallax* Klapálek, Notes Leyden Mus. 32: 44.

1923 *N. fallax* – Klapálek, Colls. zool. Baron EDM. de SELYS LONGCHAMPS 4 (2): 148.

1973 *N. luteola* – BISHOP, Monogr. Biol. 23: 224; Table 68.

1975 *N. nitida* – JEWETT, Oriental Insects 9: 131 (part).

1983 *Neoperla* spec. D – STARK, Aquatic Insects 5: 112, figs. 39–42.

Material: ♀ holotype: Java (M. C. PIEPERS; NMP). Additional specimens: Java: 1 ♀, E. Java, Idjen Plateau, Blawan, 800 m, 23.4. 1936, light; 2 ♂♂, 2 ♀♀, same locality, 950 m, VI. 1924 (DAMMERMANN; ML). W-Java: 1 ♀, Buitenzorg, VII. 1909 (v. D. WEELE; ML); 1 ♀, Buitenzorg, III. 1909 (BRYANT & PALMER; MCZ; BANKS det.: *N. pilosella* Klap.). 2 ♂♂, Salak, 800 m, Gunung Boender, 6. IV. 1931; 1 ♂, Gedeh, Tapos, 800 m, 16. X. 1932; 1 ♂, 2 ♀♀, Gedeh, Tjisaroas, Panggerango, 1000 m, 2. VI. 1932; 1 ♀, Tjibodas, 3. IX. 1931; at light; 1 ♂ in larval skin, 1 larva, Kali Dolog, Dieng, 7. VIII. 1931 (all LIEFTINCK; ML). Sumatra: 1 ♂, Kloof van Harau [550 m, near Pajukumbu, nr Fort de Kock], XI. 1913; 1 ♂, Sungal Kumbang, [Kerintji] IX. 1915; 1 ♀, Fort de Kock, II. 1914; 11 ♀♀, Sandaranagung, Kur. VII. 1915 (JACOBSON); 1 ♀, Rimbo-Pendagang, VI. 1916 (all JACOBSON; ML). 1 ♀, S. Sumatra, Kepahiang, (Sunda Exped. THIENEMANN), at light, 13. II. 1929, (on slide; ML). 2 ♀♀, Dolok Ulu, Kora Kora, 15 km NE Pematang-Siantar, 150 m, 20. IX. 1979 (ERBER; LFS). Malaysia: 10 ♂♂, 19 ♀♀, Gombak R. 15.5 mls S Kuala Lumpur, Bentong Rd., at light, VI/VIII. 1968 (BISHOP; LFS; KAWAI det.: *luteola*). 1 ♂, Lubok Tamang, Lipis District Pahang, 3500 ft, VI. 1923, F. N. C. (BMNH; on reverse of label: Raffles Museum Singapore, F[ederated] M[alay] S[tates] Museum; received as *Phanoperla minutissima*). 1 ♂, Ganong Genom Pahan 700 ft, 30. III. 1967 (BECK; CAS; JEWETT det.: *nitida*). 1 ♂, Penang Hill, 100 m, 26. VI. 1962 (ROSS & CAVAGNARO; CAS; JEWETT det.: *nitida*). 5 ♀♀, stop 254, 16 mls NE Kuala Lumpur, 1000 ft, 8. VI. 1962, (ROSS & CAVAGNARO; CAS; JEWETT det.: *nitida*). 1 ♂, Temple Park, 30 km N of Kuala Lumpur, 150 m, 15. IX. 1960 (GRESSITT; BPBM). 1 ♀, Kuala Lumpur, 24–31. XII. 1958 (QUATE; BPBM). 1 ♂, Pahang, Kuala Tahan, 15–16. XII. 1958 (QUATE; BPBM). Thailand: 1 ♂, Banna Chawang nr Nabon, 70 m, 5. IX. 1958 (GRESSITT; BPBM). Krachong Forest near Trang, 100 m, 2–VI. 1962 (ROSS & CAVAGNARO; CAS; JEWETT det.: *nitida*). 30 ♂♂, 11 ♀♀, Trang Prov., Khao-phappa Khaochang, 200 m, 1–11. I. 1964, light trap and Malaise trap (SAMUELSON; BPBM). 8 ♀♀, several larvae, including mature ♀♀ with eggs, Chiangmai Province, Doi Sutep W. of Chiangmai, small stream and waterfalls, 1140–1450 ft, adults at light (PETERS & PETERS; LFS). 1 ♂, Chiangmai, Fang, 12–19. IV. 1958 (BPBM). 1 ♂, Chiangmai, Ban-tin-doi, 310 m, 13. XI. 1957 (GRESSITT; BPBM).

Identification doubtful: 1 exuvia, LOMBOK, Sesaut, 12. IV. 1981 (ROUGEMONT; my coll.).

Wings of ♂♂ 10.0–12.5 mm, of ♀♀ 10.5–17.0 mm long. Rs with 3–4 branches. Ocelli large, little more than one diameter apart in males. Dirty yellow, no defined pattern, sometimes an ill defined central cephalic mark and tips of antennae darker.

♂: Similar to *N. luteola* except penis. Penis plump, a patch or band of little spines dorsally at tip. Inner sac with fine teeth, usually so positioned that in resting condition the larger ones are on dorsal side of penis. Everted sac very long, curved ventrally, diameter uniform, tapers only at very tip. Base of sac bare, easily visible teeth only on convex (= dorsal) side, minute ones on other side arranged in transverse lines. Largest teeth dorsally close to tip.

♀: No external modifications, except sometimes an indistinctly darker centre of S8. Vagina large, sac-shaped, with few wide concentric folds around and in front of attachment of receptacle. These large regular folds sclerotised, numerous smaller ones on posterior face of vagina soft. A V-shaped loop round end of common oviduct may be faintly visible. There are minute microtrichia in the straight portion leading to genital opening.

Eggs oval to almost spherical, 0.30–0.35 mm long. Chorion appears to be smooth but is finely punctate without order, except on anchor pole delimited by a prominent circular fold. Collar smooth, very

variable. The disc shaped anchor inserts on a small knob. Lid with clearly visible sometimes raised suture, micropyles very close to suture.

Variation: Males from Idjen Plateau have smaller ocelli further apart than usual; no other variation has been observed in males. Females are uniform, but eggs vary. Those from Sumatra and Java have wide collars and prominent lid sutures (fig. 16f), except eggs from Sandaranagung where the suture is flat and the egg stouter than usual. Specimens from Malaysia and South Thailand have narrow collars (fig. 16h). In eggs from the northernmost localities in Thailand (fig. 16i) the collar is so shortened that the knob for anchor attachment is exposed.

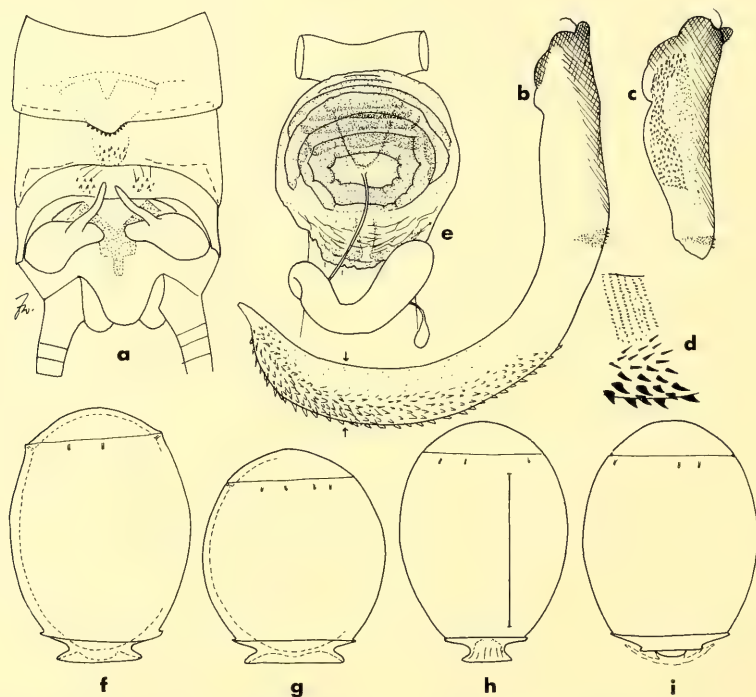


Fig. 16: *Neoperla fallax* Klapálek: Abdominal tip of ♂, (a, specimen from Lubok Tamang); b, c, penis of specimen from Trang; d, detail of penis armature at level marked by little arrows in fig. b; e, vaginal sclerites (specimen from Kuala Lumpur); f-i, eggs, scale (in h, 0.2 mm) is similar for all; f, holotype; g, specimen from Sandaranagung; h, specimen from Kuala Lumpur; i, specimen from Chiangmai.

Notes: Conspecificity of sexes is indicated by common occurrence over the entire range which is much wider than that of any other *Neoperla* in question. Whether all specimens recorded as *fallax* by Klapálek (1923) really are this species is uncertain. I have seen specimens reported as *fallax* from Malaya (Banks 1931), which are misidentified; a specimen of *fallax* misidentified as *pilosella* by Banks is listed above.

The safely identified larva of *N. fallax* is not described because to be useful larval descriptions have to be comparative and go into many details. However, adequate material of other species, except *N. lieftincki*, is not available. It was interesting to note, though, that larvae of these two closely related species differ markedly, e. g. in the occipital crest which has the usual setal row in *N. lieftincki*, while it is absent in *N. fallax*. The exuvia from Lombok is of this kind. Many similar larvae have been collected at Doi Suteh, together with ♀♀ of *N. fallax*. They are not necessarily all conspecific because similar larvae are also available to me from south India, where *N. fallax* does not occur.

II.1.4 *Neoperla lieftincki* spec. nov. (Figs. 17a–c).

Material studied: West Java: ♂ holotype, 1 ♂ paratype, Malabar Radio, 1200 m, 24. XII. 1930 (TOXOPENS; ML); 1 ♂ paratype, 4 larva, Tjisaroea Z., 1050 m, G. Panggerango, 6. VII. 1930 (LIEFTINCK, with a note stating conspecificity of adult and larvae; ML); 1 paratype, ♂ in its larval skin and 1 larva, Tjibodas, Groote Beek, 28. VII. 1930 (LIEFTINCK; ML); 1 paratype, ♂ in its larval skin, Tjibeureum [waterfall above Tjibodas], 1700 m, 28. VII. 1930 (LIEFTINCK; ML); 1 ♀ in larval skin Tjibeureum, 25. IX. 1930 (T. v. B. J.; ML).

Wings of ♂♂ 15.5–18.3 mm long, length of nymphal ♀ without cerci 23 mm. Rs with single fork or anterior branch forked again. Dull greyish brown, darker than other *Neoperla* in this group, no distinct patterns. Dark marks between ocelli and in centre of frontoclypeus in front of M-line. Wings infusate.

♂: Generally similar to *N. luteola*, except penis. Penis plump, a few spinules dorsally at apex. Everted sac about as long as tube, straight with two small spiny dorsolateral outgrowths near midlength. A dorsal band of spinules ends a short distance from tip. On the sides of the sac, there are only minute asperities. Ventrally, a band of slender spinules begins near midlength. It widens distally and expands to cover the entire tip but dorsal spinules are stouter and smaller than others.

♀: No external modifications noted, but specimen in larval skin not yet fully expanded. Vagina similar to *N. affinis* (compare fig. 18c), with parallel curved folds on anterior face of vagina, and with a pair of medially meeting lightly sclerotised rough plates below and behind the attachment of the receptacle.

Eggs distinctive, approx 0.33 mm long, elongate oval with pointed irregularly punctate lid and exposed cap-like anchor pole without collar. The simple anchor inserts in an apical pit. Polar cap smooth, delimited by fine undulating crest. Sides of egg with numerous straight bare ribs which are wide, flat. Sulci between them with single rows of funnel shaped punctures. In oblique views, rows of little pearls appear before the background of straight bare ribs. Ribs about four times wider than sulci. Micropyles simple, in sulci.

Notes: *N. lieftincki* is member of a group of three closely related species which agree in ♀ genitalia and straight everted penis sac with dorsolateral protrusions near middle. In the other members of the group, pattern of spinule placement on penis sac is the same as here, but the armature is more complex. A morphological series is observed in which the most similar forms are vicariant: *lieftincki* (Java) – *affinis* (Sumatra) – *pilosella* (Java). This might look like a series of subspecies. However, no similar clinal variation is observed in other characters and eggs differ so much that complete genetic isolation is probable. Specific status is therefore assigned to the taxa. For the larva of *N. lieftincki* compare “Notes” on *N. fallax*.

II.1.5 *Neoperla affinis* spec. nov. (Figs. 18a–d).

Material studied: Sumatra: holotype ♂, 4 ♂♂, 7 ♀♀ paratypes, Tanangtalu [PB], V. 1915 (JACOBSON; ML). Additional paratypes: 1 ♀, Médan, env. de Dolok-Baros, 2^e semestre 1905 M. MOISSINAC/Museum de Paris Sumatra 1906 M. Maindron/*rubens* KLAPÁLEK/*Neoperla*/Cotypus (see ‘Notes’) (MNHNP). 2 ♂♂, Sibolangit, (ROEP-

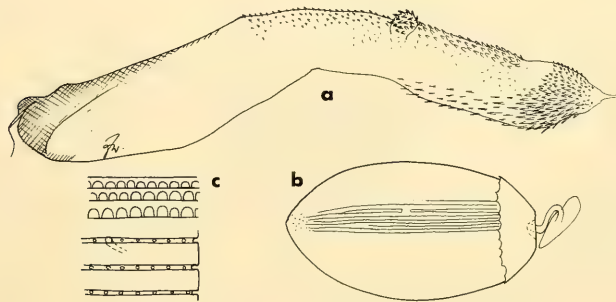


Fig. 17: *Neoperla lieftincki* spec. nov.: Everted penis (a), egg (b) and detail of chorion sculpture (c).

KE; FULMEK & KARNY; ML); 1 ♂, Gunung Teleman, V. 1917 (JACOBSON; ML); 1 ♀, Balun, Pad. Bov., VI. 1914 (JACOBSON; ML); 1 ♀, Separai, Kur., VII. 1915 (JACOBSON; ML); 1 ♀, Muara Sako [SWK], X. 1915 (JACOBSON; ML); 1 ♀, Talupuh, V. 1915 (JACOBSON; ML); 1 ♀, Tamiai, Kur. VII. 1915 (JACOBSON; ML); 1 ♂, Mt. Bandahara, Serbolangit Range, Bivouac One, 810 m, 25. VI.–5. VII. 1972 (KRIKKEN; ML); 1 ♂, Mts Dairi [W of Lake Toba], 2. V. 1981 (DIEHL; coll. SIVEC). 1 ♂, 1 ♀, Bandar Baroe [= Bandarbaru, 3.16 N/98.33 E], at light, 7. XI. 1925 (FULMECK; ML). Other material: 2 ♂♂, 1 ♀, in poor shape, each now mounted on a slide, Sibolangit, no date (LÖRTZING; ML).

Wings of ♂♂ 11.0–14.0 mm, of ♀♀ 13.0–15.5 mm long. **Rs** simply forked. Pale yellowish, ocellar rings, a diffuse patch surrounding ocelli and a median mark in front of M-line more or less darkened. The largest ♂ (from Mt. Teleman) is exceptionally dark, wings fumose, anterior branch of **Rs** forked again.

♂: Generally similar to *N. luteola* and other members of the subgroup, although process of T7 more pointed and HT with blunter median lobes than in relatives. Safe identification requires study of penis.

Penis long, moderately slender, dorsally at apex with extended patch of spinules (distal direction of their tips in fig. 18a is an artefact produced by handling during artificial eversion!). Retracted inner sac not characteristic, except when narrow basal band of teeth and separate groups of spines on outgrowths of sac happen to be visible. Everted sac narrow, tubular, almost straight, a pair of spiny spherical protrusions dorsolaterally near midlength. Near tip two dorsal and a single ventral hump. Armature consists of two bands of spinules separated by an area covered with minute asperities. Dorsal band of spinules narrow, at its base connected to wide patch of spinules on outside of penis tube. Distally it ends on the more basal of the two dorsal humps where it is widened and consists of extra large teeth. Ventral band poorly developed, consists essentially of a patch of small spinules on ventral hump. It is connected to similar but slightly larger spinules on the distal of the two dorsal humps.

♀: No external modifications. Vagina wide, strongly folded, anterior folds not sclerotised but wider and more regular than numerous small lateral and posterior folds. Seminal receptacle simple, on short raised cone which from below is supported by two medially touching and partly merging rough sclerites; each sclerite has a strong diagonal fold separating its outer lower portion from its median raised portion.

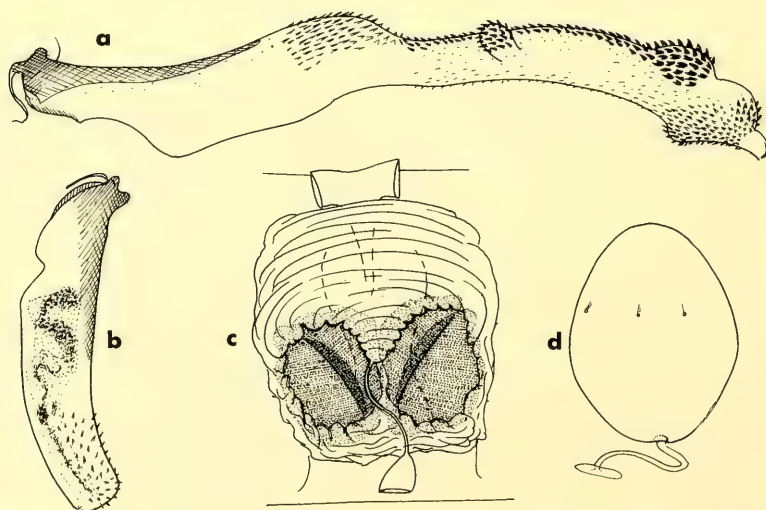


Fig. 18: *Neoperla affinis* spec. nov.: Penis in everted and contracted condition (a, b), vagina within the limits of S8 (c), egg (d).

Eggs approx. 0.24 mm long, oval, widest below middle and abruptly narrowed to anchor pole, no collar. Anchor apparently simply disk shaped, its long stalk inserted in small median depression of chorion. Chorion smooth except for fine irregular obsolete punctation visible only at magnifications near 400 \times . No visible suture of lid. Micropyles simple, far down, close to largest diameter of egg.

Notes: Association of sexes initially relied on repeated common occurrence, especially at Tanangtalu where the only other common species was *N. illiesi* which is larger and differently pigmented. Group affinities support this association. The misidentified Sumatran ♀ in the Paris Museum was not listed as and despite its label is no syntype of *N. rubens* which KLAPÁLEK had from Java only.

II.1.6 *Neoperla pilosella* KLAPÁLEK (Figs. 19a–d)

1905 *Neoperla pilosella* KLAPÁLEK, Mitt. naturhist. Mus. Hamburg 22: 103, fig. 1.

1909 *Neoperla rubens* KLAPÁLEK, Wiener ent. Ztg. 28: 221; new synonymy.

1909 *Neoperla mitis* KLAPÁLEK, Wiener ent. Ztg. 28: 221, new synonymy.

1910 *Neoperla pilosella*, *N. rubens*, *N. mitis* – KLAPÁLEK, Notes Leyden Mus., 32: (1909): 36, fig. 2; 40, fig. 4; 43

Material studied: Java: ♂ holotype of *N. pilosella*, Tjibodas, Java, 25.–28. 3. 1904 (KRAEPELIN; ZMH). ♂ lectotype, ♀ paralectotype (here designated) of *N. rubens*, Java orient. FRUHSTORFER/Greifswald/Cotype (NMP). ♀ holotype of *N. mitis*, Gedeh, Java, STAUDINGER (NMP). Additional material: 1 ♂, 1 ♀, Batavia (MCZ; BANKS det.: *N. luteola*). 2 ♂♂, 6 ♀♀, Mt. Salak, 3000 ft, 15. V. 1909; 1 ♂, Tjibodas, Mt. Gede, 7000 ft (all BRYANT & PALMER; MCZ; BANKS det.: *N. pilosella*). 1 ♂, Buitenzorg, III. 1909 (BRYANT & PALMER; MCZ); 1 ♂, 1 ♀, same date and collector (USNM; JEWETT det.: *N. luteola*); 1 ♂, Buitenzorg, VIII. 1919 (ROEPKE; ML; GEIJSKES det.: *N. luteola*). 1 ♂, 1 ♀, Tjibodas, 1400 m, 23.–30. XII. 1930 (LIEFTINCK; ML). 1 ♂, pinned (GEIJSKES det.: *N. rubens*), 1 ♂, mounted on slide (GEIJSKES det.: *N. luteola*) Mt. Gedeh, Tapos, 5–800 m, VIII. 1936 (V. D. VECHT; ML). 1 ♀, Tjibodas, Mt. Gedé, VIII. 1950 (KALSHOVEN); 1 ♀, G. Boender, Salak, 6. IV. 1931 (LIEFTINCK leg. et det.: *N. rubens*); 1 ♂, 1 ♀, Salak, G. Boender, Pasanggrahan, 800 m, at light, 24. XII. 1929 (LIEFTINCK); 1 ♂, Idjen, Blawan, 950 m, V. 1924 (DAMMERMAN; LIEFTINCK det.: *N. rubens*) (all ML).

Wings of ♂♂ 12.5–15.0 mm, of ♀♀ 15.0–18.3 mm long. Rs with single fork. Ochre; central portion of head from behind large ocelli to front end of clypeus brown, except M-line. Mark laterally poorly defined. Median band of pronotum brownish, antennal flagellum, outer face of tibiae and tarsi greyish brown.

♂: Similar to *N. luteola*, except penis. Contracted penis plump, with a (usually complete) ring of external spinules at tip. Armature of inner sac at some distance from tip, a group of few large hooks amidst a mass of small spinules. Everted sac straight, with lateral protrusions near middle. A subterminal dorsal and a larger ventral swelling each with few large hooks present, narrow hook shaped tip of sac directed to ventral side. Base of hooked section striate, apex beset with fine spinules like rest of everted sac; only those on lateral protrusions a little larger.

♀: No external modifications. An inconspicuous sclerotised loop in sac-shaped vagina. Strong parallel folds in front and on anterior face of conical central portion. Numerous delicate folds along periphery, apparently very extensible. Sides and posterior face of central cone with numerous small brown scales, not rigid. Simple receptacle at tip of cone.

Eggs approx. 0.32 mm long, chorion sculpture like in eggs of *N. lieftincki*. However, the present egg is more regularly oval, blunt lid covered by distinct meshes, punctate in their centres. There is no exposed polar cap; instead, the collar forms a narrow smooth ring surrounding attachment of apparently normal anchor.

Notes: Males with contracted penes can easily be identified by the complete (or only laterally divided) ring of external spinules on the penis, and by the few large hooks in the inner sac. Females without eggs are difficult to separate from *N. lieftincki* and *N. affinis*, although no similar arched sclerite along front end of vagina has been observed in the latter two. Eggs are easily distinguished from those of related species by shape. Similar chorion sculpture is observed in other, quite unrelated species, e. g. *N. illiesi*. I am therefore hesitating to identify as *N. pilosella* a much faded ♀ from Wai Lima, Lampongs, XI./XII. 1921 (KARNY; ML). It would be the only Sumatran specimen known.

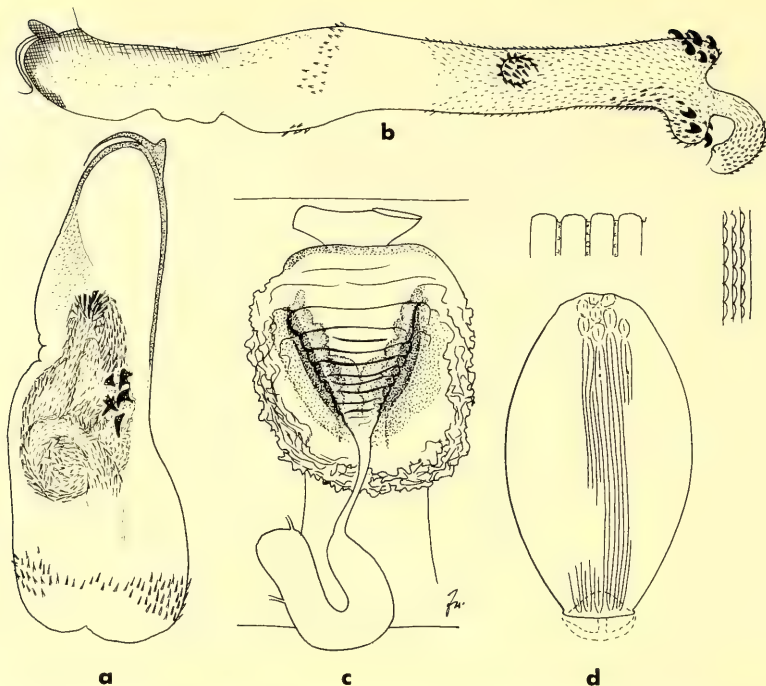


Fig. 19: *Neoperla pilosella* KLAPÁLEK: Penis in contracted and everted condition (a, b), vagina within the limits of S8 (c), egg, with details of chorion sculpture (d).

N. rubens and *N. mitis* had first been described in a key without lists of material. These followed later (KLAPÁLEK 1910), specimens listed are considered syntypes. The ♀ paralectotype of *N. rubens* has not been examined, its identity is unknown. The head of the type of *N. mitis* had been strongly damaged (KLAPÁLEK 1910); it is now missing. Compare 'Notes' on *N. affinis*!

II.2 Species of the *montivaga*-group not assigned to particular subgroups

II.2.1 *Neoperla stueberae* spec. nov. (Figs. 20a–c)

Material studied: ♂ holotype, V. 1917, 2 ♂♂ paratypes, VI. 1917, Sumatra, Gunung Teleman (JACOBSON; ML).

Large, wings 16.3–16.7 mm long. Rs with 3 branches, anterior two on a common stalk, 3rd from anastomosis. Light ochre, an indistinct line from anteromedian part of frontoclypeus to spot between small widely separate ocelli and a narrow line on occiput, along occipital suture, light brown. Appendages yellow except tibiae which are dark grey on the outside, especially in region of subgenal organ. Wings clear.

♂: Process of T7 triangular. Spinules of T8 concentrated on poorly delimited median sclerotised strip, a few also laterally from it. Usual paramedian swellings of T9 weakly expressed. Hemitergites fairly broad, simple, with rather apparent soft setae. Anterior process long and slender, bent near middle. Sternites and cerci simple.

Penis plump, opening slightly displaced to ventral side. Two small spiny laterally at tip are clearly on outside when short internal sac is completely retracted. Everted sac displaced to ventral side,

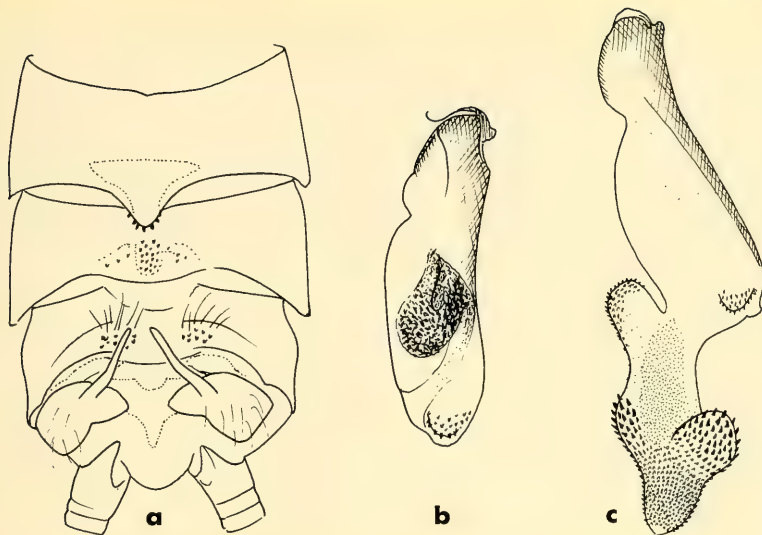


Fig. 20: *Neoperla stueberae* spec. nov.: Abdominal tip of ♂ (a), penis in contracted (b) and everted condition (c).

with single ventrobasal and two dorsolateral subterminal bulbs. Opposite the latter, ventral side also somewhat swollen. Ventrobasal bulb covered with fine spinules, sides of sac with very fine, conical apex with moderate ones. Distinctly enlarged hooks on dorsolateral bulbs and on ventral swelling.
♀: Unknown.

Notes: No close relatives of this distinct species are presently known. It is named for Fräulein GISELA STUBER, in recognition of important technical help she has provided in this and other studies.

II.2.2 *Neoperla illiesi* spec. nov. (figs. 21a–f).

Material studied: Sumatra: ♂ holotype, 2 ♂♂, 8 ♀♀ (paratypes), Tanangtalu [PB], V. 1915 (JACOBSON; ML). Additional paratypes: 1 ♀, Sungai Kumbang [Kerintji], VIII. 1915 (JACOBSON; ML). 1 ♂, NE Sumatra, Tinggi Radja, Deli, 9. IX. 1929 (V. D. MEHR MOOR; ML). G. Teleman, 1 ♂, IV. 1917, 3 ♂♂, V. 1917, 5 ♂♂, VI. 1917 (JACOBSON; ML). 1 ♀, Balighe; 1 ♀, Pangherang-Pisang, both X. 1890–III. 1891 (MODIGLIANI; MCG). 1 ♂, Bandar Baroe [= Bandarbaru, 3.16 N/98.33 E] Licht, 7. X. 1925 (FULMEK; ML).

Wings of ♂♂ 13.0–16.5 mm, of ♀♀ 15.5–21.5 mm long. Rs with 2–3 branches. Yellowish to pale ochre. A light brown spot between ocelli, no mark in front of M-line. Appendages yellow, except tibiae which are dark grey at sugenal organ and indistinctly fumose along rest of outside.

♂: Tergites 7, 8 completely simple. T9 long laterally, short medially where it has an illdefined median depression. Two groups of spinules on oblique posterior margin, close to middle. Setation simple. HT simple, anterior process short, straight, pointed in dorsal, blunt in lateral view. Cerci simple. Each of sternites 7–9 with a number of stronger setae close to posterior margin.

Penis plump, sac-shaped, almost completely filled by numerous little hooks. Everted inner sac forms a pair of dorsal knobs in straight continuation of penis tube, and a much larger bulb ventrally which carries a membranous cone with the distal opening. Delicate spicules occur on dorsal knobs, most of ventral bulb covered by much larger hooks.

♀: No external modifications. Vagina small, not nearly reaching anterior border of S8. Transparent, unsclerotised, wrinkled and apparently strongly extensible in front of seminal receptacle. There is an anchor-shaped posterior extension of the vagina. It is smooth on top, wrinkled along its posterior rounded margin and is internally supported by two very weak posteriorly widened rods rising from below.

Eggs about 0.31 mm long, oval, extremely similar to egg of *N. pilosella*. Differ by short impunctate stretch above each micropyle, and mainly by larger distinctly transverse punctures in much wider sulci. Each sulcus about half as wide as adjoining smooth ribs.

Variation: Specimens from Gunung Teleman and Sungai Kumbang are at the upper limit of the size range. They are darker than other specimens, head sometimes completely brownish (except M-line) and all of external face of tibiae dark. ♂♂ from Gunung Teleman have more slender sinuous processes of hemitergites, setation of abdominal sternites is simple, armature of penis covering all of the big bulb, but indistinct on the smaller dorsal knobs.

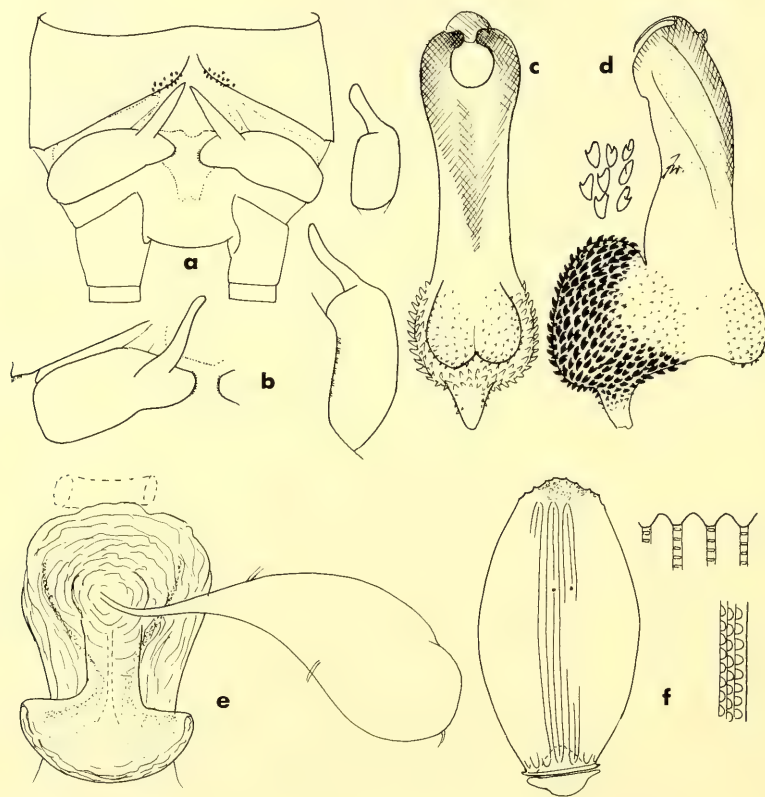


Fig. 21: *Neoperla illiesi* spec. nov.: ♂ abdominal tip and HT in profile, specimen from Tanangtalu (a), left HT of ♂ from G. Teleman in dorsal and lateral views (b), everted penis in dorsal and lateral views (c, d);, vagina (e) and egg, with details of chorion (f).

Notes: Despite resemblance to *Phanoperla* in simplicity of the male tergal modifications the present species is a typical *Neoperla*. Possibly, it is related to *N. venosa* from south India, which has also simple anterior tergites but a differently shaped penis (ZWICK 1981). Association of sexes is based on similar appearance of specimens taken together at Tanangtalu and on the good agreement of genital structures: The everted penis has anterior and posterior swellings, the vagina has anterior and posterior extensible areas.

This exceptional species is gratefully dedicated to the memory of the late Prof. JOACHIM ILLIES who first introduced me to the study of Plecoptera as supervisor of my thesis and was my fatherly colleague for many years. His untimely death in 1982 means a great loss for our science.

III. Species incertae sedis

III.1 *Neoperla tenuispina* Klapálek (Figs. 22a-c)

1921 *Neoperla tenuispina* Klapálek, Ann. Soc. ent. Belg. 61: 320.

1923 *Neoperla tenuispina* – Klapálek, Colls. Zool. Baron SELYS LONGCHAMPS 4 (2): 146, fig. 18 on p. 147.

Material: ♂ holotype, Alahan Pandjang IX. 1877/Sumatra Exp. (coll. Klapálek; NMP).

Wing approx. 14.0 mm long. Rs forked, anterior branch forked again. Largely faded, according to original description head had dark brown marks between ocelli (still faintly visible) and in the angles of the M-line. Legs yellow, except some infuscation of tibiae at subgenital organ.

♂: T7 unmodified. T8 with a median bump at posterior edge. T9 membraneous behind divided antecosta, posterior portion raised, forming two paramedian swellings with long setae and spinules. Hemitergites 10 normal except anterior processes which are very short and plump, club-shaped in dorsal view, with angular lower edge in lateral view. S9 forming a distinct short subgenital plate, remaining sternites simple.

Penis tubular, with narrow distally truncate dorsal sclerite and two well defined elongate ventrolateral sclerites. No ventral sclerite at base. Distally from dorsal sclerite an oval patch of strong spinules arranged in transverse rows. Everted sac short, with 3 basal outgrowths. Two short dorsolateral outgrowths beset with small spicules, a long ventromedian outgrowth with larger spinules on curved tip. Distal section of sac short, a ventral subterminal swelling beset with very fine spinules. The end section is a narrow filament.

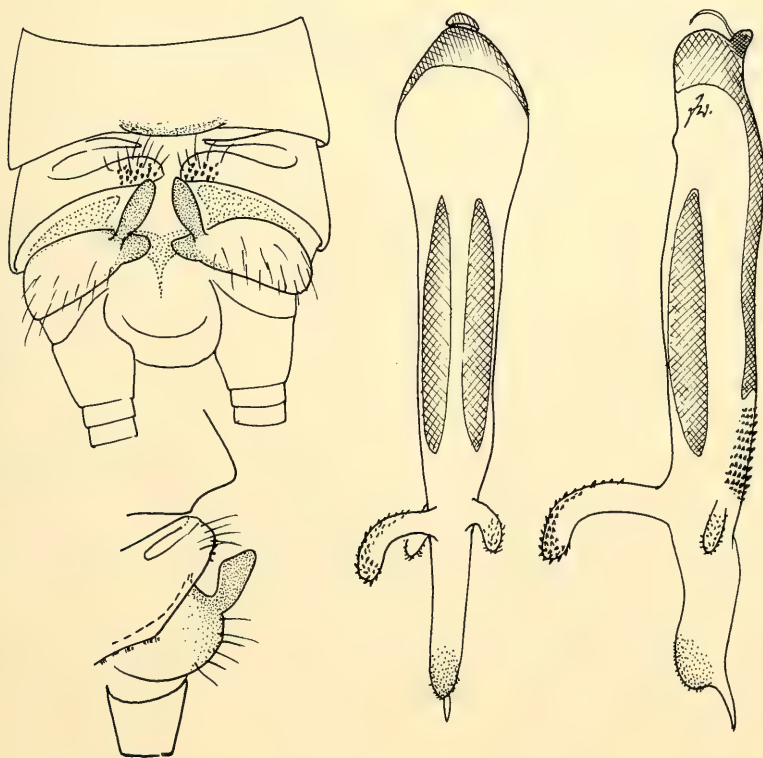


Fig. 22: *Neoperla tenuispina* Klapálek: Abdominal tip of male and everted penis in ventral and lateral views.

Notes: The original description contains no useful information. The figure published in 1923 clearly shows the present dry specimen, which KLAPÁLEK had from the Leyden Museum. *N. tenuispina* is an isolated species without close relatives, its female is not known. Structure of penis base reminds of the *clymene*-group, where secondary break-up of general sclerotisation into individual sclerites rarely occurs. However, inner penis sacs with outgrowths are very exceptional in that group and so are unmodified T7 and the peculiar shape of T8.

IV. Deletions from the Species List

Several nominal species from Sumatra and Java had been placed in *Neoperla* in the past, but are presently excluded from it.

Neoperla minutissima (ENDERLEIN, 1909) (Sumatra) and *Neoperla flaveola* KLAPÁLEK, 1909 (Java) have been transferred to *Phanoperla* (ZWICK 1982a). The name *flaveola* has been used for some misidentified species of *Neoperla* from the Asian mainland (JEWETT 1975; KAWAI 1969); compare also above, under *N. caligata*!

Neoperla modiglianina NAVÁS 1932 was described from Sumatra. The type proved to be a ♀ of *Etrocorema nigrogeniculatum* (ENDERLEIN, 1909) (ZWICK 1982b).

Formosita reducta GEIJSKES, 1952 was together with the other species of *Formosita* KLAPÁLEK, 1914 included in *Neoperla* (ILLIES 1966). While the type species of *Formosita*, *Neoperla batekayamae* OKAMOTO, 1922 (by designation of KLAPÁLEK, 1923) does in fact appear to be a *Neoperla*, *F. reducta* belongs to genus *Chinoperla*, see ZWICK & SIVEC (1980) and ZWICK (1982c).

Neoperla dolichocephala KLAPÁLEK, 1909 was originally described as one of the species "from Sumatra and Malacca", without specifications. When the species was assigned to the monotypic genus *Oodeia* (KLAPÁLEK 1921) it was surprisingly said to occur in Malakka and Java (not Sumatra). A subsequent list (KLAPÁLEK 1923) includes a ♀ from Java, a misidentified *N. jacobsoni*, see there. It was without justification labelled syntype of *N. dolichocephala*. Real *N. dolichocephala* from Malacca have also been examined. They are a distinct species not occurring in Sumatra or Java.

V. Keys

Identifications obtained with the following keys should in every case be corroborated by comparing specimens to figures and descriptions and examining characters not used in the key.

HT: male hemitergite 10; S: sternite; T: tergite.

V.1. Key to genera of Perlidae known in Sumatra and Java

- 1 Sc of front wing very short, ends in basal third of wing *Chinoperla* Zwick
- Sc normal, ending in distal half of wing 2
- 2 Cu₂ of front wing very short, its strongly curved base forks out of Cu₁ at an almost right angle *Phanoperla* Banks
- Cu₂ of front wing straight, rising at the usual acute angle, length normal 3
- 3 ♂: HT simple anteriorly curved hooks. Strong brushes of setae on metasternum and on several abdominal sternites. ♀: huge distally notched subgenital plate covers most of abdominal tip from below *Etrocorema* Klapálek
- ♂: HT forked, with medially directed plump tip and slender anterior process. Abdominal brushes of setae present or absent, never present on metathorax. ♀: subgenital plate (if present) smaller, covering at most part of S9 *Neoperla* Needham

V.2. Key to the species of *Neoperla* known from Sumatra and Java.

♀ of *N. distincta*, *N. vesperi*, *N. stueberae* and *N. tenuispina* are not known.

1	Males	2
–	Females	20
2	T7 unmodified	3
–	T7 with a process or extension	4
3	T8 unmodified. Penis wide, only a short mediobasal sclerite ventrally	<i>N. illiesi</i>
–	Distal margin of T8 slightly thickened, projecting. Penis narrow, two long ventrolateral sclerites present	<i>N. tenuispina</i>
4	Abdominal sternites without brushes of erect setae	5
–	S7, sometimes also S8, with distinct brush of erect setae	15
5	Body of HT strongly curved, a silky hair fringe on posteromedian edge	<i>N. distincta</i>
–	Body of HT straight, but sometimes with outgrowth on posteromedian face	6
6	Sclerite of T8 long, spinules on it in two rows, or in a posteriorly widened or forked row. HT and S9 often modified, penis often with an outgrowth	7
–	Sclerite on T8 variable, spinules on it forming a single narrow band or a posteriorly tapering undivided patch. HT, S9 and penis never modified as before	12
7	Penis completely sclerotised	<i>N. rigidipennis</i>
–	Penis ventrally and distally membranous, annulate	8
8	HT with large ax-shaped outgrowth covered with long setae. S9 simple. Penis gently curved, no outgrowth. Very dark species, often with blue sheen.	<i>N. aeripennis</i>
–	HT with different modifications, or unmodified; sides of basal penis sclerite with small prominent knob	9
9	Penis rectangularly bent	10
–	Penis curved or bent at blunt angle, never rectangularly bent	11
10	Process of T7 wider than long. Anterior process of HT plump, distal tapered half medially flattened. Lateral edges and median tip of S9 short, not very prominent	<i>N. caligata</i>
–	Process of T7 narrow, as wide as long. Anterior hemitergal process slender, bent. Edges of S9 with long bladeshaped apendages, median tip prominent	<i>N. sumatrana</i>
11	Process of T7 notched. HT with variable outgrowth, triangular when small, finger shaped with outwardly curved tip when large. S9 simple. Penis angularly bent, its apical appendage smooth	<i>N. aliqua</i>
–	Process of T7 entire, triangular. HT only with small posterior knob. S9 with at least angular edges, sometimes with blade shaped appendage. Penis gently curved, not bent, its appendage (if present) spiny	<i>N. propinqua</i>
12	Spinules on T8 aligned on a narrow band-shaped sclerite	13
–	Spinules on T8 scattered on a broadly triangular or rounded sclerite	14
13	Penis tube completely sclerotised, smooth. Spinules on inner sac slender, without apparent order	<i>N. primitiva</i>
–	Penis tube unsclerotised, dorsodistally with strong transverse folds. Inner sac with major hooks in two rows	<i>N. jacobsoni</i>
14	Penis slender, ventrally without basal, but with a long distal sclerite. Inner sac narrow and long, undulating	<i>N. vesperi</i>
–	Penis plump, ventrally with short basal sclerite, unsclerotised distally. Inner sac short, wide, appears as dense mass of spines without order	<i>N. stueberae</i>
15	Base of inner sac with a pair of appendages often visible at tip of unverted penis. No major hooks in armature	<i>N. luteola</i>

– Inner sac without basal extensions but outgrowths near middle (visible only when sac is everted) may be present. Often with some large hooks in armature	16
16 Near base of inner sac there are long bands of delicate long spicules and of large plump hooks. Everted sac forms almost full circle <i>N. simplicior</i>	
– Armature different, larger hooks (when present) in small clusters	17
17 Armature fairly uniform in size, no outgrowths, everted sac describes a half circle <i>N. fallax</i>	
– Inner sac straight, with outgrowths near middle	18
18 Armature of inner sac of uniform size, apex of sac simply conical <i>N. lieftincki</i>	
– Some teeth of armature distinctly larger than others. Apex of inner sac of complex shape	19
19 External spicules present only on dorsodistal edge of penis. Enlarged teeth on a long dorsal band of inner sac, largest on a dorsal subterminal swelling <i>N. affinis</i>	
– A subterminal ring of external spicules (sometimes divided on sides) on penis tube present. Armature fine except some very large hooks on dorsal and ventral subterminal swellings <i>N. pilosella</i>	
20 Distal margin of S8 a usually bilobed subgenital plate which may be small or large. Vagina narrow, elongate, base of seminal receptacle appearing like a small comma with spicules inside	21
– No subgenital plate. Modifications of S8, if present, only in the form of faint pigment marks. Base of seminal receptacle long, coiled, armed; or narrow, short, completely simple	27
21 Distal margin of S8 strongly sinuous, arched on sides so that the short almost entire subgenital plate is hardly projecting	22
– Subgenital plate variable but clearly projecting	23
22 Egg regularly oval, no collar, chorion at poles thinner than near middle <i>N. spec. AsM</i>	
– Egg drop-shaped, chorion of uniform width, an inconspicuous fold delimits flat anchor pole. Margin of narrow collar forms many short finger-like processes <i>N. spec. AsL</i>	
23 Egg elongate, oval, seemingly with two collars. Large circular grooves on surface <i>N. aliqua</i>	
– Egg shorter and plumper, surface variable, never with circular grooves; never two collar-like smooth rings present	24
24 Numerous club-shaped projections on chorion <i>N. sumatrana</i>	
– Chorion variously sculptured, without projections, except sometimes on collar	25
25 Collar absent, anchor inserts in deep groove of almost spherical egg <i>N. aeripennis</i>	
– Collar present, with finger-shaped outwardly bent outgrowths	26
26 Collar narrow, less than 10 outgrowths, circular fold surrounding collar hardly apparent. Relatively gross completely irregular punctation <i>N. caligata</i>	
– Collar wide, more than 10 outgrowths on it. Circular fold very apparent. Chorion seemingly smooth, shining; at high magnification appears a fine irregular punctation on polygonal fields delimited by smooth lines <i>N. spec. AsK</i>	
27 Vagina narrow, small, no major extensible folds. Base of seminal receptacle wide, coiled, forming a very apparent brown spiral lined with spicules. Eggs with longitudinal sulci, punctation in sulci either irregular or in two regular lateral lines	28
– Vagina with large extensible folds, transverse or more or less circular, sometimes partly sclerotised. Base of receptacle completely simple, narrow, unarmed, often not easily visible. Eggs variable, if longitudinally striate, a single row of punctures per sulcus	30
28 Armed base of receptacle short, forming approx. half circle. Eggs with few very wide irregularly punctate sulci <i>N. primitiva</i>	
– Armed section of receptacle longer forming almost complete circle. Eggs narrowly striate, punctate sulci and bare ribs of subequal width	29

- 29 Punctate meshes on lid delimited by flat smooth strips of chorion, not apparent in profile . . . *N. jacobsoni*
 – Punctate meshes on lid delimited by strongly flanged strips of chorion which are very apparent in profile
 *N. spec. AsJ*
- 30 Vagina very small, unsclerotised, shorter than S8, with an anchor shaped posterior extension behind
 receptacle *N. illiesi*
 – Vagina large, as long as S8 or even extending into S7, with very conspicuous circular folds or with
 sclerites 31
- 31 Concentric vaginal folds few, very apparent, usually sclerotised. Egg: suture of lid visible, fold surround-
 ing collar very prominent, chorion seemingly smooth *N. fallax*
 – Vaginal folds more numerous but less apparent and unsclerotised. No visible suture of lid, fold round
 collar not prominent 32
- 32 Vagina unsclerotised or small rough sclerites that may be present posteriorly largely hidden by over-
 hanging central cone to which the receptacle is attached 33
 – Central cone of vagina less large, two large brown medially confluent areas of rough sclerotisation
 behind attachment of receptacle therefore well visible 34
- 33 Egg densely striate *N. luteola*
 – Egg not striate, chorion seemingly smooth, punctate *N. simplicior*
- 34 Egg not striate, seemingly smooth *N. affinis*
 – Eggs longitudinally striate 35
- 35 Egg with exposed smooth cap at anchor pole, remaining 4/5 of surface striate *N. lieftincki*
 – Egg completely striate, its sides distinctly and regularly curved, lid blunt, anchor pole flat . . . *N. pilosella*

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